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Editor
T. Delevoryas

THE NORTH AMERICAN SUNFLOWERS (*HELIANTHUS*)

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Torrey Botanical Club

Volume 22

Editor

T. Delevoryas

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Introduction

Whereas, Kansas has a native wild flower common throughout her borders, hardy and conspicuous, of definite, unvarying and striking shape, easily sketched, moulded, and carved, having armorial capacities, ideally adapted for artistic reproduction, with its strong, distinct disk and its golden circle of clear glowing rays—a flower that a child can draw on a slate, a woman can work in silk, or a man can carve on stone or fashion in clay; and

Whereas, This flower has to all Kansans a historic symbolism which speaks of frontier days, winding trails, pathless prairies, and is full of life and glory of the past, the pride of the present, and richly emblematic of the majesty of a golden future, and is a flower which has given Kansas the worldwide name, "The Sunflower State": therefore,

Be it enacted by the Legislature of the State of Kansas: That the *Helianthus* or wild native sunflower is hereby made, designated and declared to be the state flower and floral emblem of the State of Kansas.—from the Session Laws of Kansas, June 1, 1903.

Back in 1936 I happened to be in Chicago during the heat of the presidential campaign and, during lunch, I asked Standley what were his political preferences. "Just yesterday," he remarked casually, "I did my best for the Republicans." It developed that he had had a visit from a Republican functionary who was in charge of publicity for the campaign of Governor Alf M. Landon of Kansas, the "Sunflower State."

"Doctor Standley," the man explained, "we would like you to give us some facts of general interest about the sunflower which we may use for the support of Governor Landon." "Surely," agreed Standley briskly. "The sunflower is an obnoxious weed; it impoverishes the soil upon which it grows." The man cleared his throat and smiled uneasily. "We'll skip that one, Doctor," he said. "Can you think of some way in which the sunflower might be regarded as a symbol of America's position in world affairs?" "Yes," Standley conceded, "sunflower seeds are the favorite light snack of the Russians." "Oh, no," the

> man moaned, "try again—possibly something of a parallel of the sunflower and the American people . . ." "Surely," Standley resumed, "the sunflower is a natural hybrid of uncertain parentage." "Doctor Standley," the sweating man exploded, "Can't you say anything *good* about the sunflower?" "I'm afraid not," was the smug reply. "You see, I'm a Democrat."
>
> from *My Debt to Paul C. Standley* by R. E. Woodson, Jr. in *Homage to Standley,* ed. by Louis O. Williams, Chicago Natural History Museum, 1963.

It all depends on one's point of view. The present point of view is primarily a taxonomic one. Since sunflowers are such well known plants, it may come as somewhat of a surprise that they have received so little attention from taxonomists. Perhaps this stems in part from the many hybrids in the genus which have made it difficult for the taxonomist who faced their classification to say anything good about the genus, regardless of his politics. The only previous attempt at a comprehensive treatment was Watson's "Contributions to a monograph of the genus *Helianthus*" (1929). This work has received considerable criticism, little of it in print except for that of Cockerell (1929), himself an able student of sunflowers. Watson's keys are virtually unusable; with a few exceptions he did not place the species in any order to show relationships; he did not acknowledge the existence of hybrids; he failed to give distribution maps or cite exsiccatae; and he was an extreme splitter. On the other hand, his descriptions are good, he brought together some of the widely scattered taxonomic literature, and he called attention to a number of the problems in the genus. Certainly his work has been of considerable aid.

A fitting title for this work might be "Contributions to a monograph of the genus *Helianthus,* II," for the present treatment is not a monograph, but hopefully brings us nearer to one. The title selected, in fact, is hardly adequate, for the knowledge of the genus in Canada is quite limited. Although no species occurs in Canada that is not known for the United States, the details of the variation of the Canadian plants have not been adequately studied.

Although I have done varying amounts of work with all of the species, the present treatment of certain species essentially follows the unpublished work of certain of my students and it is perhaps appropriate to list those species to which the other authors have contributed. Sarah Clevenger (1955): *H. atrorubens, carnosus, heterophyllus, laetiflorus, longifolius, occidentalis, pumilus, radula, rigidus, silphioides,* and *subrhomboideus*; Dale Smith (1957): *H. decapetalus, divaricatus, glaucophyllus, hirsutus, laevigatus, mic-*

rocephalus, and *strumosus*; William Martin (1958): *H. agrestis, angustifolius, atrorubens, carnosus, floridanus, heterophyllus, longifolius, radula*, and *salicifolius*. It should also be noted that Dr. Smith has also contributed in various ways to the understanding of many other species. In addition, in the treatment of certain other species I have relied on the published works of other former students, Robert Long and Raymond Jackson.

In several of the species I do not entirely agree with the treatments of some of these workers listed above, and in final analysis, I will have to assume the full responsibility for the interpretation presented here.

Generic Relationships

The closest relatives of *Helianthus* appear to be *Viguiera, Tithonia* and *Phoebanthus*. The separation of the first two from *Helianthus* is based almost solely on the nature of the pappus. In *Helianthus* the pappus consists of two awns, usually without squamellae, and is readily deciduous, whereas in both *Viguiera* and *Tithonia* the pappus consists of persistent awns and squamellae, or in a few species, entirely lacking. Moreover, *Tithonia* is usually characterized by rather strongly angled achenes and a fistulose peduncle. With the exception of monocephalic forms of *H. annuus* the peduncle is not noticeably swollen in *Helianthus*. The distinction between *Helianthus* and *Viguiera* breaks down completely in a few species, notably *H. similis*, so that one might justify combining the two genera, although there is certainly some convenience in having the two separate. The relationships of the three genera were discussed by Blake (1918) and there is really little to add. Subsequent study of chromosome numbers and other characters confirms the close relationship.

Chromosome numbers have been reported for four of the 11 species of *Tithonia*, all n = 17, the same as that of dipolid species of *Helianthus*. In *Viguiera* there are 8 species reported with n = 17, two with n = 34, two with n = 8, and one each with n = 12 and n = 18. Since there are nearly 150 species in the genus, it is obviously too early to make generalizations but it is perhaps significant that 17 is the most frequently reported number. It should be noted that the counts of n = 8 are both from members of section Heliomeris which is probably best considered a distinct genus (Heiser, 1963; Yates, 1967).

A limited number of intergeneric hybridizations have been attempted between various species of both *Tithonia* and *Viguiera* with *Helianthus*. With the exception of crosses involving *V. porteri*, no seeds have been secured. Sterile hybrids of *V. porteri* have been obtained with four species of *Helianthus* and one species of *Viguiera* (Heiser, 1963). However, in view of the fact that the proper generic placement of *V. porteri* is open to question, the production of these hybrids does not argue for combining the two genera.

The generic relationships of *Helianthus* need more study. In addition to evidence from chromosome numbers, it would be desirable to have information on the morphology of the chromosomes. Whether the number 17 is an original basic number or whether it has been derived through polyploidy (Heiser and Smith, 1955) is still an open question.

Phoebanthus is undoubtedly closely related to *Helianthus* and perhaps should be combined with it. The genus comprises two species endemic to Florida, somewhat similar to *H. angustifolius* but readily separable from *Helianthus* by the production of small horizontal tubers. These species also have a basic chromosome number of 17 with *P. tenuifolia* being diploid and *P. grandiflora* being tetraploid. Difficulty in growing these species in Indiana has prevented attempts at hybridization with species of *Helianthus*.

Sections

Although there has been fairly general agreement as to the generic limits of *Helianthus* since the genus was founded, there has never been any agreement upon categories between genus and species. De Candolle (1836) in his key recognized Annui; Perennes, disco atropurpureo; Perennes, disco luteo, foliis omnibus oppositis; Perennes disco luteo, foliis superioribus alternis; and Fruticosi. Torrey and Gray (1843) give six sections, "Annui, Angustifolii, Atrorubentes, Laetiflori, Corono-Solis, and Microcephali." Gray, later (1884) however, recognized only two sections, "Annuals" and "Perennials," his failure to use classical names perhaps being significant. Rydberg (1932) sets up one section of annuals and six sections of perennials for the sunflowers occurring in central North America. However, two species, *H. chartaceus* and *H. hirsutus* are assigned to both his Divaricati and Tuberosi. Watson (1929) recognizes two admittedly artificial groups based on disk corolla color, the Rubri and the Flavi. Since several species are known in which both disk flower colors may occur, this classification is of limited usefulness.

Recently I (1965a) have suggested a partitioning of the genus into four "sections" based primarily on the ability of species to hybridize although there are also some morphological characters (e.g. annual vs. perennial) that support this arrangement. I did not give formal taxonomic recognition to these "sections," nor do I propose to do so now, partly because of the feeling that formal designation might indicate a more precise understanding of relationships than had actually been attained, partly because of the feeling that formal categories between genus and species in general do not serve any great advantage, and partly because there are few or no good morphological characters on which to base sections.

The informal sections previously recognized and which are used here are as follows:

I The annuals, including a few taprooted perennials, or "Annui" (14 species).[1] With the exceptions of *H. similis, H. ludens* and *H. agrestis*, the members of this section are closely related as indicated by crossability, and probably form a phylogenetic unit. The twelve species for which chromosome numbers are known are all diploid.

II Western perennials or "Ciliares" (6 species). The five diploid members of this section have been connected by a series of artificial hybrids and thus far it has been impossible to secure hybrids of any of them with members of the "Divaricati." Morphologically, no one character separates them from the "Divaricati." There are two well defined sub-groups or series: the "Ciliares" with well defined rhizome-like roots and the "Pumili" which lack these structures.

III Eastern perennials (although two species are clearly western) or "Divaricati" (30 species). This group which includes diploids, tetraploids and hexaploids has posed the greatest difficulty in species delimitation. If I am correct in assuming that an annual genome is not present in the hexaploids, the entire group is probably monophyletic. Hybridization between nearly all species at a given ploidy level is possible and the resulting hybrids usually show good chromosome pairing and moderate to high fertility. An attempt is made here to divide this section into morphological series, partly to facilitate identification and partly to show relationships, although it must be admitted that the resulting series are probably to some extent artificial. The presence of polyploid species makes it especially difficult to establish either natural or presumed phylogenetic series since the ancestors of certain polyploids may have come from more than one series. It is possible that some other arrangement of species into series would be equally logical and attention will be called to other possibilities. Five series are recognized. (See section on species concepts for species included in each series.)

1. "Divaricati." This is a rather heterogeneous series. In an earlier work (Clevenger, 1955) *H. occidentalis*, with its nearly leafless stem, and *H. rigidus*, also often with reduced stem leaves and quite broad phyllaries, were placed with species of series 5 (Atrorubentes), but the well developed rhizomes as well as their ready hybridization with other members of series 1 have prompted their transfer. Some of the polyploid species of this series probably contain a genome from species in series 2 but since they share more morphological features with species of series 1 they are placed here.

2. "Gigantei." (Essentially the Corona-Solis of Torrey and Gray.) The five diploid members of this series form a very natural, and probably phylogenetic, group. Two of the polyploids fall naturally here, but the

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[1] If formal designation of a section is to be adopted the name Helianthus will have to be used for this section since the nomenclatural type of the genus is *Helianthus annuus*.

third, *H. resinosus*, is polymorphic and some individuals of this species seem to be more similar to species in series 1 but others to species in series 2. This situation reflects the taxonomic difficulties inherent in this group. Since in present taxonomic work a species can belong to only one series it is placed in series 2. Rydberg (1932), however, as previously mentioned, found it necessary to place the same species of *Helianthus* in two different sections, and Michener (1963) has called attention to the artificiality resulting from insistence on mutually exclusive taxa.

3. "Microcephali." Although *H. microcephalus* is not the oldest species of this series, I shall use this name since it was used by Torrey and Gray (1843) and is most appropriate. Two of the diploid species of this group, *H. microcephalus* and *H. glaucophyllus*, are clearly closely related and one or the other probably furnished a genome to the two tetraploids. However, the inclusion of *H. longifolius*, although a small headed species, may be quite artificial since it shares few other characters in common with the remaining species.

4. "Angustifolii." *Helianthus angustifolius* is a fairly distinctive species that does not fall readily into any other series. It intergrades extensively with *H. floridanus* and *H. simulans*, which therefore are placed with it in this series, but it should be pointed out that if there were not intermediates connecting *H. angustifolius* with *H. floridanus* and *H. simulans*, the latter two species could with equal justification be placed in other sections, *H. simulans* in series 2 and *H. floridanus* in series 1.

5. "Atrorubentes." Four of the five species placed here form a fairly natural alliance and probably have a recent common ancestor but the fifth, *H. carnosus*, which is quite different morphologically may not belong to the same phylogenetic group. The fact that *H. silphioides* has well developed stem leaves in contrast to the other members of this group, weakens the morphological basis of the series but there can be no doubt that it clearly belongs in the group since it is very closely related to *H. atrorubens*.

IV The South American perennials or "Fruticosi." These species have previously been revised (Heiser, 1957) and are not included in the present work. One additional species has recently been described from Peru (*H. lodicatus* Cuatr., Proc. Biol. Soc. Wash. 77:144, 1964). It was concluded earlier that in all probability the South American species are not closely related to the North American *Helianthus* but probably arose directly in South America from a viguieroid stock. I still subscribe to this view.

Species Concepts

While I admire the biological species definition of Mayr (1940, 1942), I find it difficult to apply it to any plant group with which I have worked. However, I feel that the species of *Helianthus* recognized herein, with the exception of some of the polyploids, might be termed biological species although there may be interbreeding occurring more freely between them than proponents of the biological species concept would allow.

There is now considerable information about the crossability of the species, both artificially and in nature, and it cannot be denied that this information has been useful in recognizing and delimiting species. For example, that *H. niveus* subsp. *canescens* should not be considered a variety of *H. petiolaris* first became evident through the crossing results and was later verified by additional morphological studies. However, the species are not based on barriers to crossability but on degrees of what is thought to be the genetic relationship (see discussion in Lewis, 1959). Since the nature of the species differs considerably in the different sections, and sometimes even within sections, it seems appropriate to discuss them section by section.

I Annui. With one or two exceptions, the species in this section now pose no great problems and are "good" species both morphologically and on the basis of crossing behavior. Those species which can be hybridized produce hybrids with reduced fertility, and, with one known exception, members of a given species produce fertile hybrids with each other. The one significant exception is *H. petiolaris* (Heiser, 1961a) for which a taxonomic system is inadequate to describe the morphological and crossing behavior. The annual species may hybridize in nature and one species, *H. annuus*, hybridizes rather extensively with four other species and introgression may occur. However, in view of the reduction of fertility of the hybrids there is no justification for reducing them all to a single species. The difficulties in identifying annual sunflowers are due more to extensive ecological modification of the phenotype rather than to intermediates produced through hybridization.

II Ciliares. The species of the western perennials are, for the most part, clear cut, largely perhaps because the diploid members are allopatric and there is little or no intergradation. That some of the species are potentially interbreeding, however, is indicated by hybridization studies.

III Divaricati. The eastern perennials offer the greatest problems in determining what are to be called species, for strong barriers to interbreeding have not developed and a large number of what we have chosen to call species hybridize rather freely in nature. This is true of both the dipolids and polyploids but the latter pose the greater dilemmas. Polyploidy complexes, such as exist here, of course, are notorious for their taxonomic difficulties and compromises in the recognition of species are called for. Smith (1961) and Heiser and Smith (1964) have discussed some of the problems relating to the polyploids and additional discussion will be found under the individual species in the present work.

Although most of the species in the series "Atrorubentes" need no defense, one might develop a case, based on lack of strong barriers to interbreeding

Table 1

Species of section Divaricati

A. Present treatment. B. Possible treatment

		A	B
Series	1. Divaricati	mollis (2n)	mollis
		occidentalis (2n)	occidentalis
		divaricatus (2n)	divaricatus
		decapetalus (2n)	decapetalus
		decapetalus (4n)	
		hirsutus (4n)	strumosus
		strumosus (4n)	
		strumosus (6n)	
		eggertii (6n)	
		tuberosus (6n)	tuberosus
		rigidus (6n)	
	2. Gigantei	resinosus (6n)	
		giganteus (2n)	
		grosseserratus (2n)	giganteus
		nuttallii (2n)	
		maximiliani (2n)	maximiliani
		salicifolius (2n)	salicifolius
		californicus (6n)	californicus
		schweinitzii (6n)	schweinitzii
	3. Microcephali	microcephalus (2n)	microcephalus
		glaucophyllus (2n	
		laevigatus (4n)	laevigatus
		smithii (4n)	smithii (or strumosus?)
		longifolius (2n)	longifolius
	4. Angustifolii	angustifolius (2n)	
		simulans (2n)	angustifolius
		floridanus (2n)	
	5. Atrorubentes	silphioides (2n)	
		atrorubens (2n)	atrorubens
		heterophyllus (2n)	heterophyllus
		radula (2n)	radula
		carnosus (2n)	carnosus

and some morphological intergradation for recognizing all the other taxa at a given ploidy level as a single species. This would be rather extreme, however, and even then it does not take into account the difficulty of separating certain diploids from tetraploids and tetraploids from hexaploids. To solve the latter problem one might then propose that we should have only a single species!

Obviously one can come up with other possible treatments. In Table 1 are listed those species recognized here (Column A) and a more conservative treatment (Column B) in which only 19 or 20 species would be accepted. Scheme B has some advantages in that some of the more freely hybridizing and extensively intergrading species are combined. Even so, some species, such as *H. mollis* and *H. occidentalis,* which are known to hybridize naturally with several other species are still maintained since they are for the most part well set off from other species morphologically. The second scheme also eliminates those species, *H. decapetalus* and *H. strumosus*, which include two ploidy levels. This may look more realistic on paper but it offers many disadvantages since it is often impossible to distinguish the different ploidy levels of these species without actually examining the chromosomes.

If scheme B were to be adopted it would introduce other problems. Since it is felt that names are desirable for all of the taxa listed in scheme A it would mean that many new subspecific combinations would have to be created. Although one might justify some subspecies, for example *H. atrorubens* and *H. silphioides* might be considered geographical races of one species, one could hardly consider doing the same with *H. tuberosus* and *H. strumosus* or with *H. giganteus* and *H. grosseserratus*. In fact, a strict interpretation of the biological species concept would probably result in a drastic reduction of species in many genera of flowering plants. It is doubtful that reducing the rank of these from species to subspecies would serve any practical purpose. It seems far better to tolerate some interbreeding between species, although this poses the problem as to how much interbreeding can be allowed before two taxa are considered one.

The species that are recognized in Scheme A are for the most part well marked morphologically and appear to breed more freely with their own kind rather than with other species. Discussions under the individual species will present some of the problems faced.

Infraspecific Taxa

Nearly all species are extremely variable and to attempt to provide names for all the variants is an impossible and unnecessary task. In the past varieties or forms have often been named on the basis of a single character, such as yellow vs. purple disk flowers or whorled vs. opposite leaves, frequently from a single specimen. I do not deny that these characters may be of biological significance, but our understanding of the biology of the species is hardly enhanced by naming such specimens, nor do I see that such names can be defended on the basis of usefulness. They only clutter up the literature.

An exception is provided by those variants usually based on more than one character, which have a distinct or more or less distinct distribution. These are called subspecies here, although some botanists still use variety for such geographical races. Some of the subspecies recognized by others, however, are not maintained, although this is not to deny that their authors have given the species careful study. When one studies a species intensively he may tend to magnify minor differences.

Morphology and Descriptions

In a review of a book on the mammals of North America Simpson (1959) points out that the "ranges of measurements are usually given without indication of means (and) size of samples . . . so that the real nature and limits of variation are unguessable." Alas, this criticism is also true of the present work, as well as for most other botanical monographs. Some explanation of the descriptions, therefore seems to be in order.

The descriptions are based upon herbarium specimens, field observations, and study of plants grown in the garden or the greenhouse. All but two of the North American species have been grown at Bloomington, although several of them have been from a single source. Some indication as to the minimum size of the samples can be had from an examination of the maps. It must be realized, however, that a single dot may at times represent a considerable number of specimens, since only one dot is used for each county regardless of the number of specimens examined from that county.

From our study of plants grown under greenhouse and field conditions as well as the study of plants in the field, it is apparent that nearly all species of *Helianthus* are rather plastic and hence subject to considerable environmental modification. The extremes perhaps are best illustrated by *Helianthus annuus* where in the same natural population plants may be found in flower ranging from 15 cm. to 2 m. in height, the former with short petiolate, lanceolate leaves with cuneate bases, a single head with a disk less than 1 cm. in diam., narrow phyllaries and less than 10 ray flowers and the latter with long petiolate ovate leaves with cordate bases, numerous heads with disks over 3.0 cm. in diameter with broad phyllaries and 30 or more ray flowers. Similar variation can be induced under artificial conditions in the greenhouse by regulating the pot size in which the plants are grown.

A second factor that makes giving precise measurements difficult is the developmental variation which may be seen in the leaves in which there is usually a gradual decrease in size and change in shape as they approach the inflorescence. Other examples will be given below.

A third factor that makes compiling descriptions difficult is the frequent hybridization between species. Although F_1 hybrids are usually readily recognizable as such, hybrids by backcrossing to their parents often produce characters which grade from one species into the next.

Therefore, in the present work the "normal" range of variation of the species is given, and for some characters unusual extremes are indicated by means of parentheses. It has also been necessary to resort to phrases such as "more or less" in referring to certain characters. It is possible that one may encounter specimens which will not fit all the measurements for any given species. Determination of whether such a specimen is a hybrid, an extreme environmental modification, or perhaps even a new species, requires considerable work!

Although the treatment of variation here is not statistical, it should be pointed out that in many studies of selected species previously published, information is given as to means and standard deviations or scatter diagrams are presented. These papers are cited under the individual species.

The descriptions are very brief, partly because of the use of sections and series makes it possible to eliminate those characters common to all members of a given group. Still greater economy could be effected by eliminating from the descriptions those characters given in the key. For the most part they are repeated, for one who is interested in identifying a given specimen may have to resort to reading whole descriptions rather than depending solely on the keys. Brevity has also been attained through the elimination of descriptive details about characters, which so far as is known, have little value in separating species, such as shape of ray and disk flowers.

A few general remarks about the usage of certain terms and the significance of certain characters is necessary. The underground parts of sunflowers (and of many other plants, as well), are too rarely or too incompletely collected for herbarium specimens, simply because it is easier to pull a sunflower up than it is to spend the time required to dig it up; I must confess that this is a practice of which I, myself, have been guilty at times. The nature of the underground parts—roots thickened or not, rhizome present or absent—is often quite useful in placing sunflowers into sections and series. The size of the rhizome, in turn, may be important. Some species generally have long, slender rhizomes as opposed to those which have short and thick ones. The few measurements that are given, however, are based on very few observations.

Unless otherwise stated all species are erect. Height, of course, varies greatly depending on vigor but some species are generally quite tall and others quite short so that this character may be of some importance. Many species have plants with stems either greenish or red, but in some species one or the other color is consistent or predominant. Pubescence of the stem, as well as of other parts, is quite variable in some species. Because pubescence of the stem may differ on various parts, the pubescence, unless otherwise stated, is given for the mid-stem.

The nature of the leaves and their arrangement in spite of the variability offer some of the best characters for identification. Leaves may be mostly alternate to mostly or all opposite. Vigor of the plant again plays some role in the arrangement, for depauperate individuals of some species which are normally characterized by mostly alternate leaves may have them mostly opposite. The leaf measurement as given refers to the blade and is for the larger leaves.

Although the basic inflorescence of *Helianthus* is a head, the term "inflorescence" is also used to refer to the arrangement of the heads. The arrangement, usually more or less corymbose is seldom particularly useful in the identification of species except for *H. maximiliani*. The heads may be few to numerous, depending again in part on the vigor of the plant. Some species, however, are normally few headed and are so indicated in the descriptions.

Giving a precise measurement to the peduncle offers some difficulties, for the peduncle length in an inflorescence of a single plant may vary considerably and the presence of reduced leaves which gradually become bract-like in the inflorescence makes the precise definition of peduncle difficult. Some species (e.g. *H. neglectus*), however, are characterized by rather long peduncles. Reference to the drawings will perhaps serve better in most species rather than attempts at giving actual measurements.

Although the head size may vary some on the same plant (those being produced late in the season being smaller), it is nevertheless often a very useful character in separating species. The disk diameter which is given is taken from heads in flower (excluding the ray flowers); the disk diameter increases slightly as flowering progresses and seeds mature.

The nature of the phyllaries is frequently diagnostic for certain species. The shape, size, and pubescence of the phyllaries vary somewhat from the outside to the inside and unless otherwise noted the descriptions given refer to the outer ones. Only a few species have phyllaries that are conspicuously imbricate or graduate (Blake, 1918), the majority having subequal phyllaries.

The pales of the receptacle, referred to simply as pales in the descriptions, may be either entire or deeply 3 lobed with the shape and length of the central lobe showing variation from species to species. In most species there may be some variation in a single head from the outer pales which may be shallowly 3 lobed or entire to those in the center which may be more deeply lobed.

The ray corollas seemingly offer few important characters. The number and size vary somewhat, in part correlated with the size of the head. Their color except in certain ornamental varieties of *H. annuus* and *H. debilis* is some shade of yellow. A few species have pale yellow rays whereas most other species have orange-yellow rays. Because color changes may occur on drying, ray color is of limited usefulness in herbarium material.

There is some variation from species to species in diskflower size, shape, pubescence and color, but only color is used here to any extent. The color of the lobes may be yellow, various shades of red, or purple. However, it is often difficult to recognize more than two conditions, i.e., reddish or yellowish, in dried material.

The achenes are generally rather consistent in size for a given species but since very few herbarium specimens bear mature achenes the size given in the descriptions is often based on a very limited sample. The color and mottling are usually rather variable and at present do not seem to offer diagnostic characters. The shape of the achenes of a few species (*H. anomalus*, *H. radula*, and members of the series Ciliares) is rather distinctive. A few species may have entirely glabrous achenes, but most species bear a few short hairs near the apex of the achene which are usually readily deciduous; a few species (particularly *H. deserticola* and *H. anomalus*) have rather densely pubescent achenes.

The pappus is usually of two deciduous awns, but examination of a large number of specimens of several species has shown that supplementary awns or squamellae are often present and in a few species extra scales apparently are always present (*H. anomalus*, *H. deserticola*). A more detailed study might reveal that the pappus has some diagnostic value but except for a few species little emphasis is given to it in the present account.

Illustrations

It is with some reluctance that drawings are included, for the reason that one drawing for each species is hardly adequate in a genus that includes so many variable species. It is quite possible that those who use the drawings for aid in identification will find it frustrating not to be able to match a particular specimen with a drawing. However, the drawings do serve to illustrate certain features that might otherwise require lengthier descriptions. With the hope that the user will understand that they illustrate only one aspect of some species, they are included. All of the habit sketches and leaves have been reduced approximately to the same scale (x 2/5) but there is some variation in the size employed for the phyllary and the reader will have to refer to the description for size measurements. All but two of the drawings were made by Ruth (Mrs. Dale M.) Smith.

Pollination

With the exception of *H. agrestis* and certain cultivated strains of *H. annuus*, all species of *Helianthus* are self-incompatible and cross pollination is obligate. No detailed study of pollinators has been made other than for cultivated forms of *H. annuus* (Free, 1964). However, from observations in the field and in the experimental garden it is obvious that bees, including the honey bee, are the principal pollinators. Butterflies visit sunflowers extremely rarely. The occasional visits of butterflies have usually been to the pale primose form of *H. debilis* ssp. *cucumerifolius*.

Dispersal

As is well known, many species without obvious specialized adaptations for seed dispersal have been able to attain as wide a distribution as those possessing such adaptions. In *Helianthus* the pappus in most species is readily deciduous at maturity of the seed, thus it does not aid in any obvious manner in seed dispersal; and even if it were persistent, it would probably not serve as a particularly effective means of seed dispersal. To my knowledge no detailed studies have been made of the spread of sunflowers. Man, of course, has proved to be an important agent and certainly the wide distribution of many species is largely to be explained as a result of man's activities. Since many species grow along roadsides or in railroad yards it is probable that rather distant seed dispersal within North America is possible. Moreover, the perennials with tubers or rhizomes are also spread by man as the result of roadbuilding and agricultural activities. Of course, many of the species intentionally cultivated by man have often escaped from cultivation and become established.

Before man appeared on the scene probably both birds and small mammals were important agents in dispersal, for sunflower seeds are an attractive food to both groups. Some birds in visiting mature sunflower heads may scatter achenes. Most birds to my knowledge crack sunflower achenes before eating them but it is possible that some are eaten whole and may pass through the digestive system unharmed. With the exception of being spread by man at times, it seems likely that sunflower seed dispersal is probably highly localized and it is unlikely that long-distance dispersal has been involved in extending the distributions of most of the species.

Seed Germination

It is well known that seeds of a cultivated species usually germinate more readily and more evenly than those of the most nearly related wild type, and *H. annuus* demonstrates this very clearly. Seeds of cultivated strains give germinations of or approaching 100% and generally all of them germinate readily. Under the same conditions, seeds of uncultivated forms usually give no germination or rarely as much as 20%. Most other annual species show responses similar to that of wild *H. annuus*. To secure better germination various methods have been attempted and the one found most generally successful has been to plant the seeds in pots which are then set outside for three weeks to a month where they are exposed to varying temperatures, including alternate freezing and thawing. The pots are then returned to the greenhouse. Germination is still very irregular, however, and very seldom exceeds 50%. Since this method has not proved very successful for the desert annuals (*H. anomalus, H. deserticolus,* and *H. niveus* subsp. *tephrodes*), various other methods, including wetting and drying, washing in several changes of water, and soaking for several days, have been tried but germination with any method has seldom reached 10%.

Germination of perennials shows considerable variability. *Helianthus grosseserratus* and other members of the Gigantei generally give rather high percentages after a three weeks' cold treatment, but most of the other species give very low percentages and not infrequently apparently sound seed may fail to show any germination. Needless to say, this has impeded the extent of the experimental work with some species.

Ecology and Geography

The North American species of *Helianthus* are found in virtually all parts of the United States and several species extend into Canada and a few into Mexico. They occupy a variety of habitats. Several could be classed as desert species and a few somewhat paludose at least in the early stages of growth. Most species are found in fully open habitats and a few will grow in rather dense shade. A number of species can be classed as weeds. *Helianthus annuus* which has the most extensive distribution of any species apparently grows only in areas disturbed by man. Many of the other species, both annual and perennials, have distributions that have probably been enlarged by man. At least one form, the densely pubescent race of *H. nuttallii* subsp. *parishii*, has become extinct as the result of man's activities and others may have suffered a restriction in range. Several species are intentionally cultivated by man, either for ornamental purposes or as food plants (*H. annuus* and *H. tuberosus*). No attempt has been made to indicate on the maps the extent of cultivation but escapes which have apparently become established are included and at times this gives some rather unusual distributional patterns, as seen for example in *H.* x *laetiflorus* and *H. maximiliani.*

The majority of the distributions are plotted on the county outline map of the Bureau of Census published by the United States Goverment Printing Office; the county lines have been blocked out in making the reproduction used here. Several species with wide distribution are shown on the contour maps of the United States compiled by E. H. Froeschner and R.E. Woodson, Jr., published and copyrighted by the Missouri Botanical Garden. For those species with extensive Mexican distributions Map. no. 213 of the Goode Base Map Series, Department of Geography, The University of Chicago, copyright by the University of Chicago, is used.

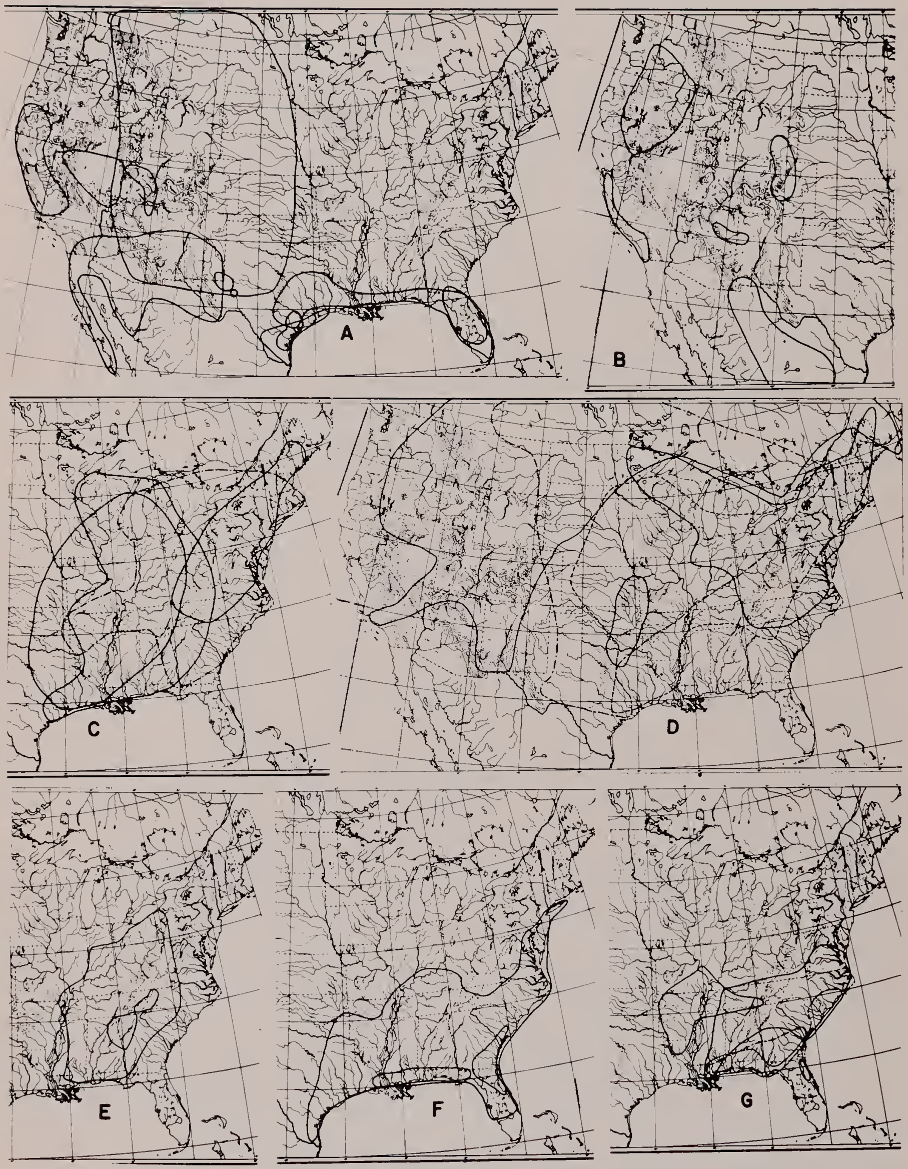
In the United States the species have been mapped with one dot to a county, although this has the disadvantage of making the species appear to be poorly distributed in states with large counties in contrast to those with small counties (Arizona as opposed to Texas, for example). In Canada and Mexico virtually all specimens have been plotted except where it would result in overlapping dots.

So far as I have been able to determine there are no fossil records of *Helianthus* so we know nothing of its past distribution or age. But if the Compositae had its origin in the Cretaceous as some have postulated and if the tribe Heliantheae is indeed the most primitive in the family (Cronquist, 1955) and if *Helianthus* were an early member of the tribe, then the genus may be of considerable age. If one knew what the most primitive extant species were, it might be of some aid in the following discussion, but even if one did, the present distribution of the primitive species need not necessarily be the same as the original distribution. There is no strong evidence for regarding any species as more primitive or older than others except that the polyploids must have been derived from extant or extinct diploids. What we do have is distributional data for the species as they now exist, and from this one may be allowed to speculate as to the past history of the genus. In this connection Woodson's discussion of *Asclepias* (1954) is most stimulating. Unfortunately, I never discussed the geography of *Helianthus* with Dr. Woodson, but certain parallels can be drawn with that of *Asclepias*. In his work Woodson assigned the North American asclepiads to six centers of concentration: Appalachian, Ozarkian, Floridian, Mexican, Californian and Antillian. The Antillian center can be eliminated from the present discussion since no sunflowers are found in that center. Also, perhaps it would be better to recognize both a Californian and western center and perhaps a Texan as well as a Mexican one.

The Annui (fig. A) are not represented in either the Appalachian or Ozarkian center except as weeds. One species, *H. bolanderi*, is Californian. Three species, *H. anomalus*, *H. deserticola* and *H. petiolaris*, can be recognized as western or southwestern, and *H. annuus* probably should be assigned to the same center. *Helianthus niveus* has one subspecies in Baja California and two that are southwestern. By far the greatest number of annual species occurs in Texas, but a distinction must be made between western Texas with *H. paradoxus*, *H. neglectus*, *H. ludens*, all with very restricted distributions, and eastern Texas with *H. praecox*, *H. argophyllus*, and *H. debilis*. The last named species also has races in Florida, and with the exception of *H. agrestis*, whose relationships may not be with the other annual species, is the only Floridian species. These distributions might be interpreted as indicating an origin in the southwest with considerable radiation there and a recent spread to the more youthful coastal areas of Texas and Florida as well as considerable spread eastward of *H. annuus*, *H. debilis*, and *H. petiolaris* in historic time as a result of man's activities. Additional discussion may be found under certain of the individual species.

The section Ciliares (fig. B) is confined to the west. The species of the series Pumili are found in the Rockies, the northwest, and California, whereas the species of the series Ciliares are southwestern and Mexican. Unfortunately, none of these species has yet been associated with any of the Tertiary floras of the western United States. While the possibility exists that they are very young species, I would be more inclined to consider most of them among the most ancient still existing in the genus.

The section Divaricati has a great concentration of species in the Appalachian region and secondary centers in the Ozarks and Florida. Only two species are clearly western. In the series Divaricati, one species *H. decapetalus* (2n & 4n) can be considered Appalachian. Three, *H. divaricati* (2n), *H.*



Figs. A-G, Generalized distribution of the diploid species of *Helianthus*. (What are considered recent introductions have been omitted.) Fig. A. Annuals, excluding *H. annuus*, *H. ludens*, and *H. similis*. Fig. B. Section Ciliares. Figs. C-G, Section Divaricati. Fig. C. Series Divaricati, including putative diploids of *H. decapetalus*. Fig. D. Series Gigantei. Fig. E. Series Microcephali. Fig. F. Series Angustifolii. Fig. G. Series Atrorubentes.

hirsutus (4n) and *H. strumosus* (4n & 6n), must be assigned to both the Appalachian and Ozarkian centers. Three taxa, *H. occidentalis* (2n), *H. mollis* (2n), and *H. rigidus* subsp. *rigidus* (6n), are Ozarkian. The other subspecies of *H. rigidus* is western and in view of the various possibilities of the origin of the two subspecies (Clevenger and Heiser, 1963) it is somewhat pointless to attempt to say which subspecies has the more ancient distribution. Two species, *H. tuberosus* (6n), because of its very wide distribution and *H. eggertii* (6n), which falls somewhat between the Ozarkian and Appalachian area, can hardly be assigned to any center.

The series Gigantei has three Appalachian representatives, *H. giganteus* (2n), *H. resinosus* (6n), and *H. schweinitzii* (6n). That *H. giganteus* could be a recent immigrant here from the north, however, is a possibility (see discussion under that species). *Helianthus salicifolius* (2n) is fairly clearly Ozarkian, and *H. grosseserratus* (2n) and *H. maximiliani* probably should be placed in the same center (fig. D). *Helianthus nuttallii* (2n) is western, although one subspecies, *rydbergii*, has a distribution approaching that of *Asclepias nuttalliana*, which Woodson considers Ozarkian. There is also a perplexing Canadian element in this species. Another subspecies, *parishii*, which is limited to southern California, poses a problem to which I shall return after discussing the other sections. *Helianthus californicus* (6n) is of course Californian. It is of some interest that there are closely related polyploid species in this section on opposite sides of the continent, and this fact may indicate considerable age for the basic species of this group.

All of the species of the Microcephali are centered in the Appalachians (fig. E), and the members of the Angustifolii are perhaps best considered Floridian (fig. F).

The series Atrorubentes, all diploids (fig. G), has species in all three eastern centers. *Helianthus carnosus*, the most divergent member of the series and perhaps artificially placed here, is confined to Florida and *H. radula* can also be placed in the Floridian center. It is of some interest that these two species which are extremes for several characters in the genus are both Floridian. Woodson's statement in regard to *Asclepias* is of some pertinence in this connection. "The great diversification of *Asclepias* in the Floridian center may be due in part to the fluctuating 'Orange Island' archipelago in early Tertiary, and partly to the southward migration to the Coastal plain (as it became available) of certain Appalachian elements in late Tertiary and Pleistocene . . . . " Perhaps both very effective isolation and rather unusual environmental conditions have interacted to produce the morphological extremes found in *Helianthus* in Florida.

Helianthus heterophyllus has a distribution rather similar to that of *H. radula* except that it is absent from peninsular Florida. Of the remaining two species in the series, one, *H. atrorubens*, is clearly Appalachian and the other, *H. silphioides*, could be assigned to the Ozarkian center. These last two species are closely related, if not co-specific, and along with their near relative, *H. radula*, a Floridian species, they provide somewhat of a parallel to Woodson's original three subspecies of *Asclepias tuberosa*. Woodson has suggested that "the incursions of the sea and glaciation in the Cretaceous and Cenozoic times might logically be assumed as contributory to the evolution of their respective subspecies."

Woodson, after considering the distributions of all of the species, concludes that the "ancestral homeland of *Asclepias* in North America is in the Appalachian and Ozark highlands, paleozoic land masses upon which the genus may well have been represented in some form as early as Cretaceous . . . . With the draining of the Cretaceous seas from the Rocky Mountain geosyncline, the Western United States and Mexico gradually received Asclepiad immigrants from the east . . . ." A similar conclusion might be reached for *Helianthus*, but I am not convinced that other interpretations might not be equally valid. For example, there are some reasons for thinking that the genus may be southwestern in origin. Its close generic relatives, *Viguiera* and *Tithonia*, are not found in the eastern United States but do reach the American southwest, and I consider it more likely that *Helianthus* comes from a viguieroid stock rather than the reverse. Secondly, if as I assume, the tap-rooted perennial condition is the primitive one, it may be significant that several of the tap-rooted perennials are southwestern. Finally, an explanation of the pan-continental distribution of the Gigantei must be provided. Is one to interpret this as indicating an eastern origin with *H. nuttallii* being a recently derived western species with an isolated subspecies, *parishii*, in southern California? Might it not be read in the other direction with *parishii* being a relic race and ssp. *nuttallii* an old species which in turn was ancestral to *H. giganteus* and *H. grosseserratus*? If a southwestern origin for the genus is accepted, it probably means that the eastern species are post Cretaceous in origin, and while it is probably true that the Appalachians and the Ozarks have served as centers, then these centers all stem from postglacial times. Finally, the reader should be cautioned again to distinguish the facts (the present day distribution of the species) from the speculation (how these species attained these distributions).

Area and Ploidy

In view of the past interest in this subject (Stebbins, 1950; Johnson *et al*, 1965), a comparison of the distribution of the polyploids and diploids is in order. Two problems, however, immediately present themselves. Because of the somewhat different nature of the polyploids and the diploids are we actually comparing equivalent taxa? Secondly, in order to have valid comparisons the distribution of the polyploid must be contrasted with its progenitors, and the progenitors are not known with absolute certainty for any of the polyploids. With these problems understood but not solved, it nevertheless may be of some interest to attempt comparisons.

There are twelve polyploids known at present in the genus. One of these, *H. ciliaris*, is in the Ciliares and shows a much greater distribution than *H. arizonensis*, the diploid species most similar to it morphologically. The range of *H. ciliaris*, however, is only slightly greater than that of *H. laciniatus*, the other diploid which also may have furnished a genome to the polyploid.

The remainder of the polyploids fall within the section Divaricati and the majority of these in the series Divaricati. Of these *H. decapetalus* provides the most valid comparison for here we have a diploid and a tetraploid that appear very similar morphologically. As can be seen from the map (#25) the suspected diploids occupy a slightly more limited area than do the presumed tetraploids, and moreover the tetraploids have a greater extension into area that was once glaciated.

Helianthus hirsutus, a tetraploid, has a very wide distribution, but it is no greater, nor does it occupy a greater extent in glaciated territory, than that of *H. divaricatus*, the diploid to which it appears the most closely related. One hexaploid, *H. eggertii*, occupies a very restricted area. On the other hand three species, *H. rigidus*, and *H. tuberosus*, both hexaploids, and *H. strumosus*, which includes both tetraploids and hexaploids, occupy very extensive areas, greater than any of the diploids which might be postulated as parents. In terms of total area occupied they must be considered as some of the most successful perennial species. It should also be noted that these three species and *H. hirsutus* are among the perennials that are most active in colonizing disturbed areas.

In the series Gigantei the two hexaploids, *H. californicus* and *H. resinosus*, although occupying fairly sizable areas, do not have nearly as large a range as their nearest morphological counterparts among the diploids, *H. nuttallii* and *H. giganteus*, respectively. The third polyploid in this series, also hexaploid, *H. schweinitzii*, has a very localized distribution.

The only other series to include polyploids, both tetraploids, is the Microcephali. *Helianthus laevigatus* does not occupy a large area and *H. smithii* is known from very few stations whereas the diploid *H. microcephalus*, which may have served as one of its parents, has a very extensive range.

In summary it can be stated that four polyploids have fairly extensive ranges, three occupy small areas and the remainder are of somewhat intermediate ranges. It is, of course, possible that those species with very restricted distribution are recently-formed species which have not yet had time to reach their full potential. Obviously, no clear-cut generalizations are in order in regard to polyploidy and geographical distribution in the genus *Helianthus*.

Exsiccatae

One of the criticisms of Watson's "monograph" was his failure to cite herbarium specimens. Since I am guilty of the same sin, some defense or excuse is in order. Although the citation of long lists of specimens is an aspect of mongraphs that has been severely criticized by non-taxonomic botanists, their inclusion is completely justified since they serve as documentation of the species as interpreted by the monographer and make it possible for other workers to verify his concept as well as to check the distribution of each specimen. Obviously it is of great use to those who are attempting to compile floras since they can immediately learn the distribution of a particular species.

It is probably true, however, that of the very few who use a monograph, still fewer make use of the exsiccatae. As an example of the infrequency of their use I might cite that several years ago in my treatment of *H. debilis* (1956) it was stated that a mimeographed list of the exsiccatae would be sent upon request to anyone interested in having one. There was not a single request. In view of the great space required to cite exsiccatae and the infrequency of their use, it is difficult to defend their inclusion with the present high cost of publication. On the other hand, information as to the source of a particular dot on the map is available. First of all, specimens are cited and an index to the exsiccatae is included in the theses by Long (1954), Clevenger (1955), Smith (1957), and Martin (1958). All of these, except Clevenger's are available on microfilm. The list of specimens used in our experimental work is cited in the individual paper in which the reports are given. Finally, the full list of specimens examined is preserved in manuscript form in the herbarium of Indiana University so that it should be possible to obtain information about any particular species by writing to the Curator of the Herbarium at Indiana University.

A portion or all of the specimens of *Helianthus* has been examined from the following institutions: University of Arkansas, University of Arizona, University of California (Berkeley), University of California (Davis), Chicago Natural History Museum, Duke University, Department of Agriculture of Canada, University of Florida, Florida State University, University of Georgia, Gray Herbarium of Harvard University, University of Illinois, Illinois State Museum, Indiana University, University of Iowa, University of Kansas, Kansas State University, University of Kentucky, University of Michigan, Michigan State University, Milwaukee Public Museum, University of Minnesota, Missouri Botanical Garden, University of Nebraska, University of Nevada, University of New Mexico, New York Botanical Garden, University of North Carolina, North Carolina State University, Oberlin College, Ohio State University, Philadelphia Academy of Natural

Sciences, Southern Methodist University, Dudley Herbarium of Stanford University, University of Tennessee, University of Texas, United States National Herbarium, Inter-Mountain Herbarium of the University of Utah, University of West Virginia, University of Wisconsin, and Rocky Mountain Herbarium of the University of Wyoming.

European herbaria have not been consulted. This is perhaps unimportant for an American genus except that many of the early species were described by European botanists. While effort has been made to assure that the correct name is attached to every species, it is possible that some changes may be necessary in the future. Sunflowers were early grown as ornamentals in Europe and hybridization took place. Some of these hybrids or hybrid derivatives were later described as species. It has been impossible to be absolutely certain of the disposition to be made of some of the names. In the systematic treatment the word "type" or "T.", unless otherwise indicated, refers to the holotype.

At least ten percent of the specimens examined for this study should probably be discarded either because of the inadequacy of the collecting data or the specimen or frequently both.

Keys

The "moment of truth" comes when one attempts to make a key to species. I have heard it stated by taxonomists that if "good" species are present then one should be able to key them out without difficulty. Either the species of *Helianthus* are not good or the previous statement is in error, for it is difficult to make a satisfactory key. That this is not simply my inadequacy may be indicated by the following quote from Mason (1957). "*Helianthus* is a genus . . . of many species of bewildering variability. . . . The polymorphy of the group is such that, in the construction of a key, diagnostic characters seem to vanish, and the liberal use of such qualifying terms as 'frequently,' 'usually,' 'more or less,' 'seldom,' and so on, is demanded. In our key this is evident, not only between the two perennial species, but also between the annual and perennial groups, wherein difficulty was encountered in finding reliable characters to bolster the not always clear-cut duration of life span."

Watson's (1929) key, as stated in the introduction, is practically impossible to use. Keys in various recent floras (Fernald, 1950; Gleason, 1952) are on the whole quite good, but it must be remembered that they are not attempting treatment of but a limited number of species.

It is hoped that the use of sections and series may simplify the matter of keying, but the user may frequently find that he will have to try his specimen in more than one of these. Emphasis is often placed on underground characters, although it is realized that these are often lacking in specimens. It has also frequently been necessary to resort to the use of geographical range as a supplementary character in the keys and the reader, of course, will realize that it is possible that a given specimen may be found outside of the known range.

No attempt has been made to provide a key to the many hybrids found in the genus. It is hardly necessary to point out that if individuals are encountered that do not fit any species there is a possibility that they may be hybrids. Occasionally these may "key out" to one or the other of the parent species (or unfortunately, at times, to a species that isn't even involved in the parentage!) and then by comparison with the description and the list of known hybrids it may be possible to determine what other species is likely involved. The identification of hybrids is, obviously, facilitated if the other species which occur in the area are known.

A separate key is not provided for cultivated sunflowers, since these should key out readily in the keys already provided. Attention should be called to the fact that two of the most widely cultivated sunflowers, *H.* x *laetiflorus* and *H.* x *multiflorus* are considered hybrids, and are not found in the keys.

Some people have looked forward to the publication of this work as making it easy to identify sunflowers. I am sorry to say that they will probably be disappointed. The greatest contribution perhaps is an explanation as to why sunflowers are difficult.

Hybridization

The role of hybridization in the genus has been the subject of numerous papers so that detailed consideration of it in the present work is hardly necessary. The discovery of another interspecific hybrid combination in the genus would scarcely be noteworthy. In fact, the number of papers that have appeared on hybridization in the genus is almost a source of embarrassment.

The occurrence of both hybrids and hybrid swarms is well documented but the extent of introgression is far from clear (Heiser, 1961b). To prove that two species hybridize is relatively simple but the proof for introgression is more elusive. Let us, for example, assume that species A hybridizes with species B and that species B shows in part of its range characteristics that could have been derived from species A. How is the situation to be explained? (1) The homologous characters might simply be the result of independent mutations. However, the greater the number of characters involved the less likely they can be accounted for on the basis of independent mutations. (2) Another possible explanation is that that portion of species B with some characteristics of A is an ancestral form of the two species which has retained characteristics of both species. (3) That characters can be transferred from one species of plant to another by repeated backcrossing is, of course, quite clear from work of plant breeders. Therefore, although absolute proof may be lacking, introgression seems to be the most likely explanation of certain types of variation encountered in some species of *Helianthus*. My contention has been that hybridization followed by introgression has not only increased the morphological variability of certain species but has also had ecological consequences and allowed certain species, notably *H. annuus*, to increase their range. Experimental evidence that introgression can provide genotypes allowing a species to expand into new environments has recently been furnished by Lewontin and Birch (1966).

Among the annuals only *H. annuus* is known to hybridize to any great extent with other species, for the reason that most of the other species are allopatric with each other. All of the artificial hybrids between annual species show reduction in fertility, probably resulting from the structural difference in chromosomes so that one might consider that structural rearrangement of chromosomes has played an important role in the speciation. The reduced fertility is seen both in pollen stainability and seed set, with the latter generally running lower than that of the pollen stainability. For example, pollen stainability in hybrids of *H. annuus* x *H. petiolaris* usually ranges from 5 to 20%; seed set of the hybrids in the experimental field with both parents growing nearby ranges from 1 to 10%, seed set on controlled backcrosses ranges from 0 to 2% and sister crosses give less than 1% seed set. Pollen stainability is probably the more direct indication of the degree of structural differences in the chromosomes of the two parents since the pollen production directly follows meiosis whereas seed set requires several events. . . . the production of a viable egg, successful pollination and fertilization.

Sterility, of course, is not the only barrier to gene exchange in the annuals since many species have their peak of blooming at different seasons and also show ecological differences. These two barriers are also prominent among many of the perennials, but strong sterility barriers are poorly developed in the perennials; this difference between perennials and annuals has been discussed by Grant (1963). Structural differences in the chromosomes of most of the species of the section Divaricati have not occurred and pollen stainability percentages in the artificial and natural hybrids both within and between series of the Divaricati often approach those of the parents. Seed set in the perennials seems to be a less reliable measure of fertility, for many species of the perennials, both in nature and in controlled crosses, often fail to produce a full complement of seed. Obviously in the annuals good seed set would be a necessity, whereas in most perennials there would be less selective value for good seed set since the rhizomes provide an efficient means of survival and increase. Long (1960) in his study found variation in seed set from year to year. In only one cross did he secure 100% good seed set, and in some of his crosses no seeds were formed. It is quite possible that the latter could represent incompatible combinations, since incompatibility systems operate in the perennial species as well as the annuals. It is also possible that self incompatibility could account for the failure of some plants in nature to set seed, for an extensive population may sometimes represent a single clone.

Although the species of perennials often form hybrids as fertile or nearly as fertile in nature as the parents, this does not necessarily destroy their consideration as biological species. It is generally more difficult to secure seed set between species than it is to secure seed between sister plants of the same species, *H. giganteus* x *H. grosseserratus* being the most notable exception. Repeated effort has been necessary to secure artificial hybrids between several of the eastern perennials, for example *H. divaricatus* and *H. microcephalus* (Smith and Guard, 1958). Although little experimental evidence is available (Heiser, Martin and Smith, 1960) it also seems possible that there may be a differential growth of a species' own pollen over that of foreign pollen. Pollen of both *H. mollis* and *H. occidentalis* was applied to the head of a plant of *H. mollis* which was known to be compatible with both pollen donors. Sixty-one seeds were secured from this cross. Only 5 seeds germinated and these gave rise to four *mollis* plants and one hybrid. The poor germination of the seed of this particular plant is not exceptional among the perennials. A similar experiment was tried with *H. grosseserratus* and *H. mollis*. A head of *H. grosseserratus* pollinated with both *H. grosseserratus* and *H. mollis* gave 19 seeds from which 17 plants were secured, all of which were *H. grosseserratus*. The cross the other way (*H. mollis* with pollen of *mollis* & *grosseserratus*) gave 63 seeds but all failed to germinate.

Although there are numerous papers on hybrids in the perennials, this is partly the result of detailed search for hybrids. My opinion is that while hybrids are not uncommon, they actually represent only a small percentage of the plants of the eastern United States. Moreover, these hybrids nearly always occur in areas recently disturbed by man. The putative natural hybrids known for each species are listed under the individual species in the systematic treatment.

It was mentioned earlier that it has been difficult to secure hybrids between species belonging to different sections and in the few crosses where intersectional hybrids have been secured they are mostly sterile. Hybrids with a few exceptions are fairly readily secured between homoploid species within a given section. Interspecific hybrids of section Annui show moderate to great reduction in fertility, whereas hybrids between perennial species within each section show only moderate to practically no reduction in fertility. Although not all possible interspecific hybrid combinations have been attempted, enough have been made to allow the generalizations made above. The artificial hybrids have been described in a series of papers by us (Heiser, Martin, and Smith, 1962; Heiser and Smith, 1964; Heiser, 1965a) and others (see references in Heiser *et al*, 1962). The artificial hybrids previously secured plus a few additional ones made in recent year are listed under the appropriate species in the present treatment. Certain hybrids described in the European literature are not included, for there is some question regarding the identification of the parental species. The work of Georgieva-Todorova is discussed by Heiser (1965). Marchenko (1962) has reported hybrids of *H. annuus* x *tuberosus*, *H. annuus* x *macrophyllus* and *H. annuus* x *H. subcanescens*. His *H. macrophyllus*, which he indicates to be hexaploid, is probably either *H. tuberosus* or *H. strumosus* but his *H. subcanescens*, which is considered a synonym of *H. tuberosus* in the present work, is more of a problem. In one place (p. 317) he implies that it is a hexaploid but in another (p. 328) he indicates that it probably has 16 pairs and one univalent.

Nomenclature of Hybrids

From the standpoint of the taxonomist, hybridization is an annoyance; for not only does it often result in species with fuzzy boundaries, but it also poses problems as to what nomenclatural treatment, if any, should be given to the hybrids. The International Code states that hybrids "may be designated by a formula and, whenever it seems useful or necessary, by a name . . ." and a note is appended that "in general greater precision will be achieved with less danger of confusion if formulae rather than names are used for such hybrids."

Additional hybrids have recently been reported by G. Pustovoit (1967. Distant (interspecific) hybridization in sunflowers. Proc. 2*nd* Internat. Sunflower Conference. Morden, Manitoba. p. 82-99.). It is impossible to give an evaluation of these hybrids since it is apparent that we are not calling the species by the same names. In 1967 I grew 23 samples of sunflowers sent to me by Mrs. Pustovoit, and I agreed with her specific determinations on only four of them; fourteen of her "species" I considered hybrids or hybrid derivatives involving two to several species. Among the samples was one labeled "*Helianthus demmovi*" (no authority given), a specific name unknown to me. Plants grown from seeds sent under this name all proved to be *Heliopsis helianthoides* (L.) Sweet. Mrs. Pustovoit has reported the chromosome number of this species as n=17 (1966. Interspecific hybridization as a method of sunflower selection. Eng. transl. in Soviet Genetics, vol. 2, no. 1: 33-39.) I found the plants to be n=14, agreeing with the number previously reported for *Heliopsis helianthoides*.

Mrs. Y. Georgieva-Todorova has reported a "hybrid" between *Helianthus annuus* and *Onopordon acanthium* (Plant Science, Sofia. 3:3-13. 1966). In order to secure the "hybrid" she reports that it is first necessary to graft the sunflower onto *Xanthium italicum*. Photographs of the "hybrids" look like forms of *H. annuus* to me but are not identical with the maternal parent. My information on the work was derived from personal conversations with Mrs. Georgieva. She has also presented an idiogram of the chromosomes of *H. annuus* (A karyological study of the cultivated sunflower, *Helianthus annuus*. Institute of Genetics and Plant Breeding, Academy of Agricultural Sciences, Sofia. pp. 85-90. 1966.)

The naming of hybrids is still the subject of considerable discussion (Grass, 1963; Little, 1960; Rowley, 1961, 1964) and while there is no complete agreement, the adoption of formulae rather than names seems more generally acceptable. I have briefly discussed the reason for using formulae for hybrids in *Helianthus* elsewhere (Heiser, 1961b) and have adopted that policy in the present work with two exceptions.

The two exceptions are *H.* x *multiflorus* and *laetiflorus*. Both of these hybrids are fairly widely grown as ornamentals and their names are well established in the literature. The former is rather unusual among *Helianthus* hybrids in that it is a triploid and completely sterile; hence there is no problem as to the taxonomic handling of segregates. *Helianthus* x *laetiflorus,* on the other hand, shows considerable variation and fits the Code's definition of a nothomorph.

The problem remains of how to treat introgressants or hybrid derivatives (Li, 1957; Hardin, 1958). The simplest solution and often the most sensible is not to use names. In the present work we have used a formula for what is thought to be an F_1 hybrid or for plants reasonably intermediate between two species. For the annotation of herbarium specimens we have frequently used the > symbol for what appears to be a hybrid derivative in which the features of one putative parent are predominant.

Phylogeny

While it is likely that some species have retained more characters from remote common ancestors than have others, I know of no certain way of determining what these characters are. The method proposed by Wagner (1961) which is "to determine the generalized or primitive characters on the principle that characters found in most or all of a number of related taxa are inherited essentially unchanged from the common ancestor" is of some interest, but it could at times give rather misleading results, for the reason that those species with new and superior characters might proliferate rapidly and in time come to outnumber those species with the primitive character state.

For purposes of determining the primitive versus advanced state, Wagner's method uses the species as the units for comparison. Probably in many genera, and certainly in *Helianthus,* the species are hardly equivalent entities. Attention has already been called to the different nature of the species in the annuals and perennials. Moreover, it would hardly seem appropriate to include polyploids along with diploids in such a tabulation.

Let us examine a few characters in *Helianthus.* A fairly simple and presumably clear-cut one is afforded by the ray flowers. The only species consistently with reduced ray flowers or lacking them completely is *H. radula.* It is highly probable that the reduction or loss of ray flowers in *H. radula* is derived rather than primitive. Whether or not the ancestor of *Helianthus* had ray flowers need not concern us here.

Leaf arrangement poses a somewhat more difficult problem. In a very few species the leaves remain opposite on the whole plant. In a number of species the leaves become alternate in or near the inflorescence and in the majority of species the leaves are mostly alternate. A similar situation holds in *Viguiera*, which is probably the nearest relative of *Helianthus*. According to Wagner's method the plants with mostly alternate leaves would have to be scored as primitive for this character, whereas those with all the leaves opposite would be regarded as most advanced. Exactly the reverse may be true since the lowermost leaves of all sunflowers are opposite and it might be reasonable to assume that the shift was from plants with all leaves opposite to those with leaves becoming alternate, as Cronquist (1955) has postulated for the Compositae as a whole.

Elsewhere (1965), admittedly without much evidence, I have stated that perhaps the tap-rooted perennial condition in *Helianthus* is primitive, and that the tap-rooted annuals and perennials with rhizomes are derived. There are at the most six species that could be considered tap-rooted perennials. There are 13 tap-rooted species which are strict annuals whereas there are some 28 species with rhizomes, 12 species of which are polyploid. If we turn to the closely related genus, *Viguiera*, we are not given much help for Blake (1918) points out that the underground system is known for only one third of the species.

The annual species, as might be expected, are subject to more rapid evolutionary change than are the perennials. The establishment of new plants in the perennials, particularly in those species of more or less stable habitats, is probably a very slow process. How long the perennials may live in nature is not known, but the same plants of several perennial species have persisted in the experimental garden at Bloomington for ten years and Dr. C. C. Deam had several specimens that were far older in his garden at Bluffton, Indiana. The annuals tend not only to produce more seeds per plant than do most of the perennials but also to have seeds that mature more readily. Although there are no specialized structures on the achenes for fruit dispersal in the genus, in the annuals the heads dry more rapidly and the pales tend to spread apart somewhat allowing more rapid falling of the achenes from the head. Moreover, the annuals are species of open habitats, often disturbed sites, and may build up huge populations under favorable circumstances. Since the habitat of the annuals is open to rapid change, there are probably far greater fluctuations in population size than in most of the perennials. Among the perennials, certain polyploids, chiefly *H. tuberosus*, *H. strumosus*, and *H. hirsutus*, approach the annuals in ability to invade disturbed sites.

While a phylogenetic chart might be constructed using the method advocated by Wagner (1961), it would necessitate a lot of arbitrary decisions as to what is primitive and advanced as seen from two of the examples. However, as Turrill (1942) has pointed out, phylogeny is the sugar coating of the bitter pill of taxonomic work and while I shall not attempt to present a phylogenetic diagram for the whole genus, perhaps I should be allowed some speculation. First, I think that with the exception of a very few species, which are so indicated under the discussion of species, that the subgenera represent phylogenetic groupings. I am not certain that all of the series are monophyletic but the series Atrorubentes, with the possible exception of *H. carnosus*, and the diploid members of the Gigantei are probably good monophyletic groupings. It is also obvious that certain species pairs are closely related and came from a recent common ancestor. Further speculation concerning relationships is presented under the section on geography and under the discussion of various species.

"Newer" Approaches

Numerical taxonomy—Since I have carried on numerical taxonomic studies with another genus (Heiser, Soria and Burton, 1965), it may be asked why such studies have not been made with *Helianthus*. The answers are threefold. (1) The amount of time required would be considerable. In many respects the stage has just now been reached for a numerical taxonomic analysis of the genus, since a thorough understanding of the characters to be used is required before one can begin to make a numerical comparison. (2) While a numerical taxonomic analysis might be of some interest, it would hardly add greatly to an understanding of the genus nor would it be likely to give us any "better" classification. (3) There is also considerable question as to how to conduct such a study on a large genus complicated by both interspecific hybridizations and polyploidy. Should an attempt be made to include all herbarium specimens that could be secured, or at least a reasonably large number, so as to have rather complete geographical coverage of all species? The individual specimens would thus be treated as the operational taxonomic units. If this were done it would be an immense task but it is perhaps the most objective method. Presumably after correlations were run one would obtain certain clusters which would correspond more or less to species. But what of the hybrids and polyploids? From my previous experience with numerical taxonomy certain of these might cluster with one or the other of their parents, others might come out as distinct taxa. It is quite likely that rather similar hybrids, such as *H. grosseserratus* x *divaricatus* and *H. giganteus* x *divaricatus*, would come out as more closely related to each other than to their respective parents. While in one sense of the word this might give us a natural classification, in another sense, it would certainly be highly "unnatural."

A second possibility, somewhat less objective perhaps, would be to start with the species which are recognized, which would then be the operational taxonomic units, eliminating from consideration those obvious hybrids and perhaps polyploid taxa as well. The amount of work involved would be far less than with the first method and one presumably would then get clusters of related taxa which would bring together those taxa which share the greatest number of features in common. Determining if the resulting relationships are the same as those which are proposed here would be of interest but it would not be more objective as far as the basic taxa are concerned since these would have already been accepted before beginning the analysis.

Anatomical studies—No anatomical work has been carried out in connection with the present revision. Anatomical studies have long been used in taxonomic work and as such they are most valuable in separating higher categories. As species characters anatomical differences are sometimes found to separate species that are well marked morphologically. Thus it is unlikely that anatomical features would provide characters to separate the many difficult and intergrading species of *Helianthus*. On the other hand, an anatomical study might provide characters that would serve to help distinguish the sections or series in the genus.

Biochemical systematics—In recent years an aura of glamour has surrounded the use of chemical characters in taxonomic work. Obviously, the taxonomist should use all possible characters, thus it is important that chemical characters be utilized. It is sometimes overlooked, however, that chemical characters are no different from morphological characters for taxonomic purposes. Some may be common to all members of a genus, they may vary from species to species, some may even vary within a single species. Thus chemical characters may be no better than morphological characters either in identification or in attempting to trace phylogeny, and they usually require more elaborate means of analysis than do morphological characters. It is always possible, however, that they may serve when morphological or cytogenetic information is inadequate or lacking; and it was with this hope that certain preliminary chemical studies were undertaken, for it would be highly desirable to find additional characters to justify the sections recognized here and to show the derivation of the polyploid taxa.

In an earlier paper (Heiser, 1965) mention was made of the reaction of the ligules when immersed in a KOH solution. Ligules of some species show color changes, probably indication of the presence of a chalcone, whereas those of other species give no reaction. Some additional observations have since been made, and as a result it is necessary to correct some of the previous reports as well as give certain new results.

All species of the section Annui have been tested except *H. ludens* and no color changes were observed in the majority of the species (species numbers 2 through 9 in the present treatment). Some specimens tested of both *H. anomalus* and *H. paradoxus* gave no reaction and some showed a color change but only on the narrowed basal portion of the ligule. Material of *H. agrestis* was somewhat variable, some showing no change, others giving a reaction at the base or a weak color change extending one-fourth the length of the ligule. *Helianthus similis* gave a strong reaction extending about one-third the length of the ligule.

All the perennial species (sections Ciliares and Divaricati) except *H. radula* have been tested. With three exceptions they showed a color change extending from one fourth to the full length of the ligule. In both *H. angustifolius* and *H. simulans* ligules from some plants showed a color change, whereas plants from other geographical sources did not. All material of *H. mollis*, as previously reported, showed no color change.

Chromatograms were run on several species, and a spot was detected in the perennials which was not present in the annuals. Although much more work needs to be done before definite conclusions are drawn, it seems apparent that with very few exceptions a pigment is characteristic of the perennials which is lacking or poorly developed in the annuals. It is also of some interest that apparently some variation exists within certain species for this character.

Helianthus tuberosus has long been known to contain inulin. Apparently observations have never been made on other species of *Helianthus*, although it is known that inulin is widely distributed in the Compositae (Holm, 1931; McDonald, 1946). Therefore, examination was made for the presence of inulin in a number of species. The method used was to place small sections of roots, stems, and tubers, if present, in 70% ethyl alcohol which is known to crystallize inulin. Then after two weeks or longer, free hand sections were made, and a drop of choralhydrate solution, which makes the radical markings on the crystals more distinct, was added previous to microscopic examination.

Crystals similar to those seen in *H. tuberosus* were observed in all but one of the species of section Divaricati (species numbers 21, 23, 24, 25, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 42, 43, 44, 46, 47, and 49 in the present treatment). The exception was *H. occidentalis*. Parts from three different plants of one strain of this species were collected for the test on August 25 and again on September 15. Other perennial species in the garden collected on these dates showed inulin.

In section Ciliares both *H. ciliaris* and *H. laciniatus* showed inulin crystals whereas they were not seen in either *H. gracilentus* nor *H. pumilus.* Only six species of section Annui were examined (*H. agrestis, H. annuus, H. argophyllus, H. debilis, H. niveus* and *H. paradoxus*) and inulin was not detected in any of them.

Since as Holm (1931) points out, inulin may be present in some roots but absent from others in the same sample and apparently it may be of limited duration in the stem and connected with certain seasons, it would be premature to conclude that inulin does not occur in those species in which it was not detected. However, the results are suggestive, and with the exception of *H. occidentalis* where its absence is difficult to explain, the correlation seems to be that inulin is absent in the strict taprooted species, whether perennial or annual.

Some preliminary work on chromatography of leaves was carried out by Dr. Dale Smith and also by Dr. Ralph Alston. Both found that there was little clear-cut evidence of distinctive substances, and this approach has not been pursued.

It is, of course, possible that a study of proteins might provide answers to some of the problems concerning phylogeny in the genus, but such studies would probably contribute little of significance to the "species problems."

Economic Importance

By far the most important species commercially is *H. annuus* which is widely grown both as an oil plant and as an ornamental. The only other species grown as a food plant is *H. tuberosus.* References to the use of these species will be found in the discussion under the species. In addition to *H. annuus,* several other species have ornamental value and are occasionally seen in gardens. The principal species employed are the two annuals: *H. argophyllus* (the silvery-leafed sunflower), *H. debilis* ssp. *cucumerifolius* (the cucumber-leafed sunflower), and several perennials: *H. maximiliani, H. mollis, H. rigidus, H. salicifolius* (the willow-leafed sunflower), and the hybrids, *H.* x *laetiflorus* and *H.* x *multiflorus.*

Problems for Future Studies

Watson in 1929 closed his contributions to a monograph with five "Subjects for Further Study."

(1) *H. strumosus.* This "species" still presents problems which are discussed in the present taxonomic treatment. However, the knowledge that it is a polyploid and possibly polyphyletic provides more insight into the problems concerning it.

(2) *H. rigidus.* The identity of those *rigidus* plants with yellow disk flowers or with well developed tubers was his concern. Such plants

probably owe this origin to genes from *H. tuberosus* by way of *H.* x *laetiflorus.*

(3) *H. laetiflorus.* The problems Watson raises vanish once it is realized that this taxon owes its origin to hybridization of *H. rigidus* and *H. tuberosus.*

(4) His statement that the whole group of tuber-bearing sunflowers will have to be minutely studied still applies. He apparently did not realize that *H. tuberosus* is a variable species and that characters of the tubers may show considerable variation just as do other characters of the species.

(5) He points out that the states of Minnesota, Wisconsin, Indiana, Ohio, and Pennsylvania contain specimens of bewildering variability which he was not able to dispose of satisfactorily. It is now quite clear that this bewildering array results from interspecific hybridization and polyploidy.

Although many of the problems brought up by Watson have been, more or less, satisfactorily resolved, it seems appropriate that several new problems which have presented themselves be mentioned at this point.

(1) More study needs to be devoted to the sunflowers of certain geographical areas. Canada has already been mentioned. A second area that needs more work is the southeast where there is a bewildering assemblage of intergrading species and it is possible that other sunflowers of this area may actually deserve the ranking of a species. Additional field work in western Texas and New Mexico might reveal other highly endemic species of this area.

(2) The origin of *H. tuberosus* and the related hexaploids needs more study. Although it seems fairly certain that these species contain two genomes from species of Section Divaricati the origin of the third genome is still far from certain, although it seems likely that it is also derived from the Divaricati (see discussion under *H. tuberosus*).

(3) With three significant exceptions the relationships of most of the species are now fairly well understood. *Helianthus similis* and *H. ludens* are both little known species and rather atypical for *Helianthus.* Neither species has been grown and thus no crosses have been attempted and the chromosome numbers have not been determined. *Helianthus agrestis,* on the other hand, has received considerable study but all that can be said is that it does not appear closely related to any other species of the genus. Equally interesting would be to learn more about the realtionships of *Heliomeris porteri* (A. Gray) Ckll. (*Viguiera porteri*) which might with some justification be considered a species of *Helianthus* (Heiser, 1963). Although *Heliomeris porteri* and *Helianthus*

agrestis are rather dissimilar in many ways, both are annuals, have conspicuously ciliate lower leaf margins and both may have tuberculate margined achenes.

(4) Another basic problem that deserves more consideration is the origin of the haploid chromosome number of the genus. Is seventeen an original basic number or did it arise through allopolyploidy?

Acknowledgments

Many individuals have been most helpful to us in furnishing seeds or specimens during the course of this study; and although the list of names is far too long to include here, their contributions are gratefully acknowledged as are those of the various students who have assisted at one time or another in various aspects of the investigation. Particular tribute is due to Mrs. Barbara Norby, Mr. Alvin Reeves, and Mr. Donald Burton, who served as research assistants for several years. My wife and family must also be singled out. Often they have had to sit in the hot sun while I stopped the car to investigate a patch of roadside sunflowers. My wife has also helped considerably with the manuscript. To the curators of the herbaria thanks are extended for the loan of the specimens in their care and for their patience, for more than once specimen had to be borrowed a second time.

The research program has been supported in part by grants from the National Science Foundation for several years. Some of the early work was also aided by grants from the American Philosophical Society and the National Academy of Sciences. Indiana University has most generously provided facilities and time for research, and particular thanks go to Dr. Ralph Cleland and Mrs. Virginia Flack of that institution. Special mention must also be made of Dr. Edgar Anderson, who once told me that if I looked into sunflowers I might discover something interesting and thus is directly responsible for my making a study of this genus.

Systematic Treatment

Key to Sections

Annuals, or rarely tap rooted perennials—I Annui, p. 35
Perennials
    Plants from tap roots or long creeping roots; western United States and Mexico—II Ciliares, p. 84
    Plants from rhizomes, tubers, or crown buds; species mostly eastern and central North America—III Divaricati, p. 99

Section I. Annui

There are no distinct morphological characters other than the prevailing annual condition which can be used to delimit this section. In most species the majority of the leaves are alternate, commonly ovate, and with few exceptions long petiolate. The disk flowers most frequently are reddish or purplish, but several species are known with yellow disk flowers. The disk may be somewhat more flat than in the perennial species, and in a number of species is larger than that of the perennials. In several species the middle cusp of the pale is somewhat more elongate than in most perennials and varies from glabrous to densely pubescent. If formal sections are adopted, according to the Code this section would bear the name Helianthus, since it contains the type species of the genus , *H. annuus*.

Key to Species

Phyllaries usually over 4 mm. wide, ovate or oblong-ovate, frequently abruptly attenuate; larger leaves over 10 cm. broad, cordate or subcordate; plants commonly 1.5 to 4.0 m. tall

    Leaves, phyllaries and stems hispid, rarely somewhat hirsute; leaves usually serrate .... 7. *H. annuus*

    Leaves, phyllaries and stems with dense silvery white pubescence; leaves usually entire or serrulate .... 8. *H. argophyllus*

Phyllaries usually 4 mm. or less broad, usually lanceolate, gradually attenuate; larger leaves usually less than 12 cm. broad, cuneate, truncate or cordate; plants commonly less than 2.0 m. tall

  Tips of pales in center of head densely white bearded

    Leaves, phyllaries, and stems densely canescent; leaves whitish to grayish .... 2. *H. niveus*

    Leaves, phyllaries and stems strigulose to hispid, rarely somewhat hiruste or subglabrous; leaves green or bluish-green

      Larger leaves usually twice or more as long as broad, usually deltoid-lanceolate to lanceolate, truncate to cuneate; phyllaries short attenuate .... 5. *H. petiolaris*

Larger leaves usually less than twice as long as broad, lanceolate to deltoid-ovate to ovate, truncate to cordate; phyllaries short to long attenuate

  Phyllaries long attenuate, exceeding disk; leaves subentire to serrulate; stems hispid....................................6. *H. neglectus*

  Phyllaries short attenuate, scarcely exceeding disk; leaves serrate to serrulate; stems hispid to hirsute.......................... 4. *H. praecox*

Tips of pales in center of head glabrous to hispid at tips but not densely white bearded

Pales conspicuously exceeding disk-flowers; phyllaries hirsute......9. *H. bolanderi*

Pales equalling or only slightly exceeding disk-flowers; phyllaries variously pubescent to glabrous

  Leaves very rough hispid with conspicuous hairs; phyllaries usually exceeding disk; achenes densely pubescent; Utah, Nevada and northern Arizona

    Phyllaries greatly exceeding disk; trichomes of leaves and stems scattered; achenes over 5 mm. long; scales of the pappus linear or linear-lanceolate..11. *H. anomalus*

    Phyllaries slightly exceeding disk; trichomes of leaves and stems dense; achenes to 5 mm. long; some of pappus scales ovate........10. *H. deserticola*

  Leaves variously pubescent to glabrous, if hispid, hairs not conspicuous; phyllaries equalling or exceeding disk; achenes glabrous or densely pubescent; not known for Utah, Nevada and northern Arizona

    Leaves densely canescent, tomentose, or villous, at least beneath; pappus of two awns and usually several smaller scales; southwestern United States and Mexico

      Leaves mostly alternate, canescent or tomentose, nearly equally so on both surfaces, smooth to the touch, usually truncate to cuneate; disk corollas usually red or purple tipped....2. *H. niveus*

      Leaves mostly opposite, lower surface densely villous, upper surface less so and somewhat rough, usually cordate to subcordate; disk corollas yellow.........................1. *H. similis*

    Leaves hispid or strigose to glabrous; pappus usually of 2 awns only; Florida to New Mexico

      Leaves lanceolate to ovate lanceolate, cuneate

        Disk flowers entirely yellow; leaves somewhat strigose; plants less than 1 m. tall...................14. *H. ludens*

        Disk flowers with red or purple lobes; plants usually over 1.5 m. tall, of wet, not sandy soil

          Stems nearly glabrous, usually glaucous; base of leaf and petiole ciliate with prominent white trichomes; Florida and Georgia.........13. *H. agrestis*

          Stems usually somewhat hispid, not glaucous; base of leaf and petiole not prominently ciliate; Texas ....12. *H. paradoxus*

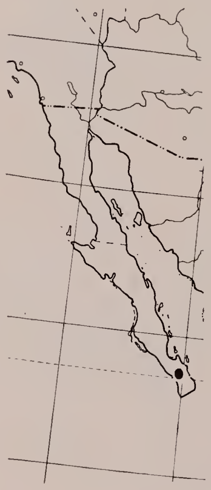
Leaves deltoid-ovate, rarely ovate-lanceolate, cuneate, truncate, or cordate; plants usually of sandy soils, usually less than 1.5 m. tall, sometimes prostrate

Leaves gradually tapering to tip; phyllaries short acuminate to long attenuate, usually not more than 3 mm. wide; Fla. to Texas........................ 3. *H. debilis*

Leaves often with constriction near middle; phyllaries short acuminate, sometimes more than 3 mm. broad; Texas.....................................4. *H. praecox*

1. Helianthus similis (Brandegee) Blake, Contri. Gray Herb., n.s. 54:189. 1918.

Viguiera similis Brandegee, Zoe 5:260. 1908. (T.: Baja Calif., Sierra de San Francisquito, *T. S. Brandegee,* Oct. 18, 1890. UC!)



Map 1. *Helianthus similis*

Spreading perennial shrub, root unknown, stem slightly tomentose, glabrate, to 1.2 m. tall; leaves opposite or uppermost subopposite, ovate, long acuminate, cordate at base, shallowly and regularly serrate, villous to tomentose and greenish above, white-villous to tomentose below, to 16 cm. long by 9 cm. wide, petiole to 2 cm. long; heads few, disk up to 1 cm. broad; peduncles 2-8 cm. long; phyllaries linear-lanceolate to lanceolate, ca. 1 cm. long and 1.5 mm. wide, acuminate; pales entire, somewhat keeled, hispidulous on mid-line; disk flowers yellow, sparingly pubescent on tube and densely so on lobes; pappus of two awns and several squamellae; achenes 2.5 mm. long, nearly glabrous.

Chromosome number: not known

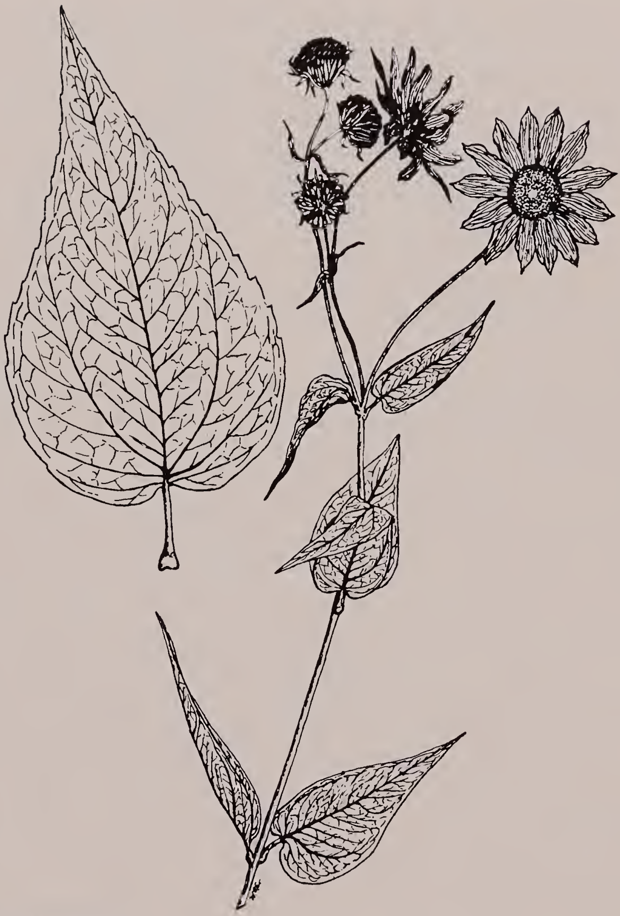


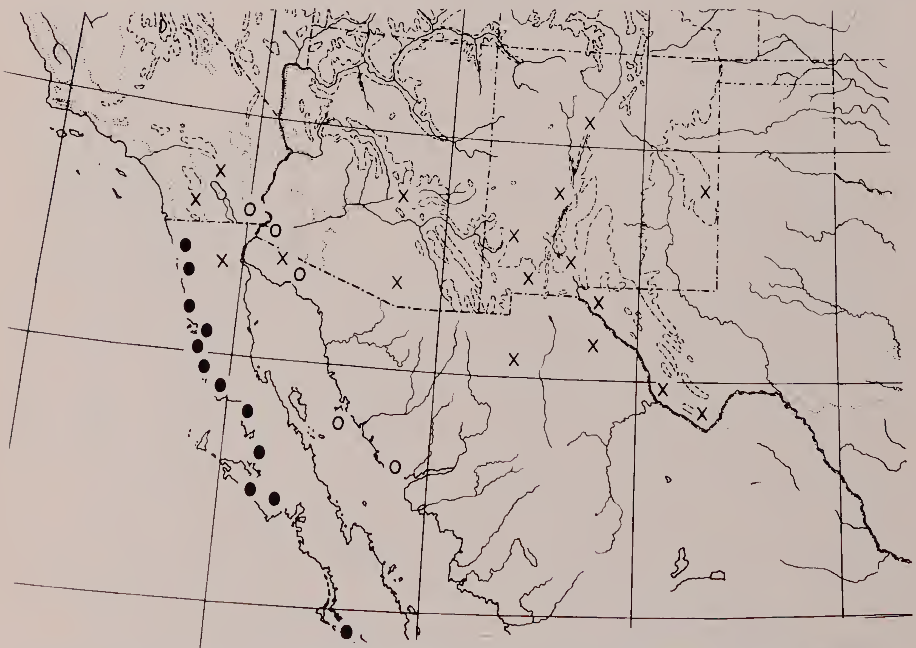
Fig. 1. *Helianthus similis*

Distribution: Southern Baja California, 1500-2000 m. In addition to the type, I have seen two other specimens: east of Todos Santos *Alexander* and *Kellogg 2402* (UC, US) and Sierra El Taste, *Carter* and *Chisaki 3507* (IND).

Brandegee pointed out the close resemblance of this species to *Viguiera tomentosa*. Blake (1918) in his revision of the latter genus transferred it to *Helianthus* since it possessed a deciduous pappus. However, in spite of that I feel that it is much more closely related to *Viguiera* than to *Helianthus* and retain it here only because technically it "keys" to *Helianthus*. It does not appear to be closely related to any species of *Helianthus* although the characteristics of the heads are somewhat similar to those of *H. niveus* subsp. *niveus*. It would be desirable to have living material in order that crosses could be attempted with representatives of both genera. The key is based on the assumption that the species has a tap root, but this is not necessarily true.

2. Helianthus niveus (Benth.) Brandegee, Proc. Calif. Acad. II. 2:173. 1889.

Encelia nivea Benth. Bot. Sulph. 27. 1844. (T.: Baja California, San Quentin, *Hinds* K. Photo GH!)



Map 2. *Helianthus niveus*. Solid dots, ssp. *niveus*; O, ssp. *tephrodes*; X, ssp. *canescens*

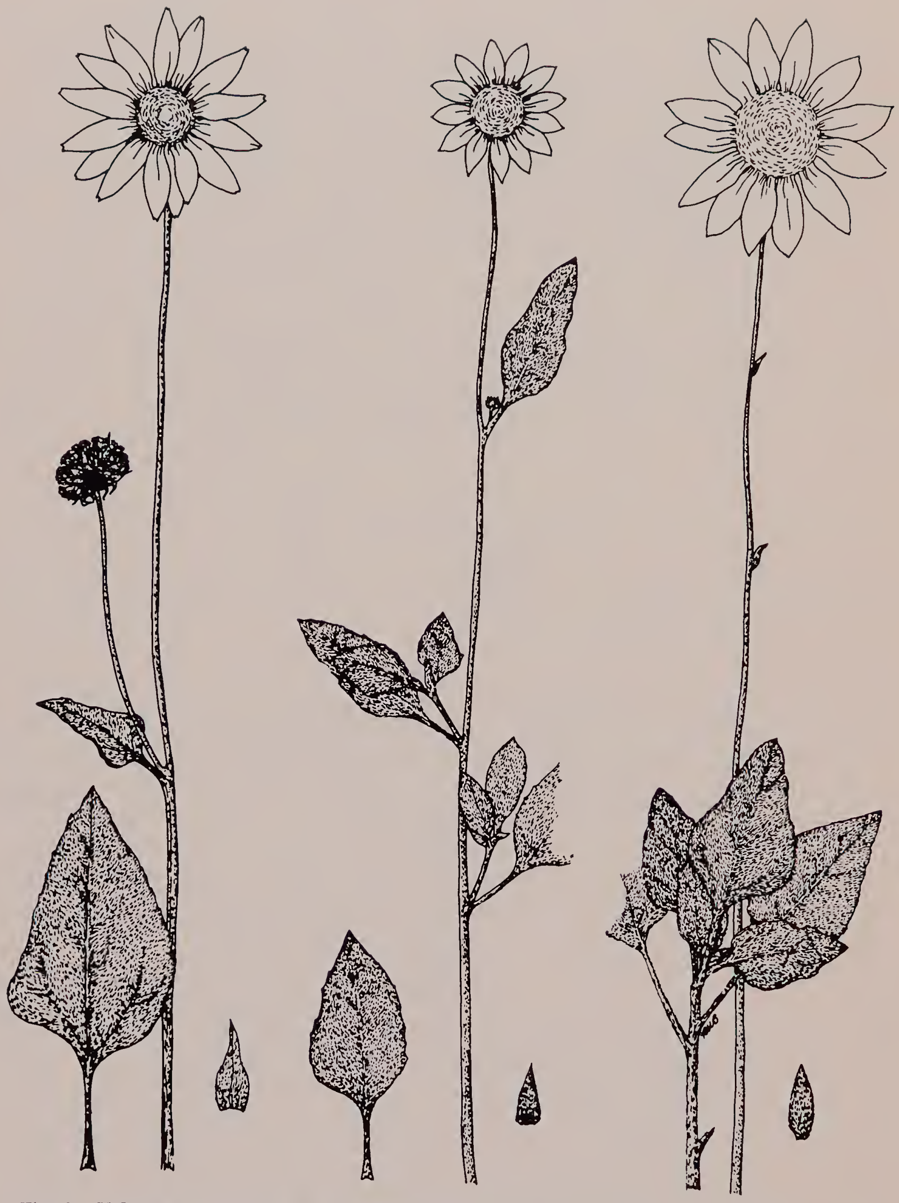


Fig. 2. *Helianthus niveus*; left, ssp. *canus*; center, ssp. *niveus*; right, ssp. *tephrodes*

Annual or perennial to 1.5 m. tall, stem sericeous-villous to strigose; leaves lanceolate to ovate, cuneate to subcordate at base, acute or obtuse at tip, occasionally somewhat fleshy, densely canescent to sericeous-villous, short to long petiolate; phyllaries linear-lanceolate to lanceolate, acute, canescent to villous, nearly equaling to slightly exceeding the disks; rays 1.2-2.5 cm. long; disk 0.8-2.8 cm. in diam.; achenes 3-8 mm. long, rather narrow, densely villous with long hairs to sparingly pubescent; pappus generally of 2 awns with squamellae present.

Chromosome number: n = 17.

Key to Subspecies

Central pales of chaff merely hispid to glabrous; leaves to 7.0 cm. long, densely sericeous-villous; phyllaries not exceeding disk; plants somewhat decumbent or shrubby, usually perennial

  Phyllaries densely woolly at base or tomentose with ciliate margins, usually outermost reflexed; leaves seldom over 3 cm. broad; disks 1.2-1.8 cm. in diam. . 2 a. *H. niveus* ssp. *niveus*

  Phyllaries evenly white-canescent, not reflexed; leaves more than 3 cm. broad; disks 1.4-2.8 cm. in diam. . . . . 2 b. *H. niveus* ssp. *tephrodes*

Central pales of chaff usually conspicuously white bearded; leaves to 12 cm. long, sparingly to densely canescent; phyllaries equalling or slightly exceeding disk; plants erect herbs, usually annual . . . . 2 c. *H. niveus* ssp. *canescens*

2a Helianthus niveus subsp. niveus

H. dealbatus Gray. Syn Fl. N. Am. 1^2:280. 1884. (T.: Baja Calif. *Belding*, GH!)[2]

Perennial from long tap root, somewhat shrubby, erect or decumbent, .3-1.0 m. tall; stem appressed white- to grayish- sericeous-villous, glabrate and woody below; leaves nearly all opposite or upper alternate, spathulate, ovate or ovate-lanceolate, entire or undulate to crisped, 2.0-5.0 cm. long, 1.5-3.0 cm. wide, appressed white- to grayish-sericeous-villous; petioles scarcely distinct to 3.0 cm. long; heads generally solitary on short to long peduncles; phyllaries 2-3 mm. wide; lobes of disk-corolla from reddish-purple to nearly yellow; pales entire or shallowly 3-cuspidate; achenes (3-)4(-5) mm. long, sparingly pubescent; pappus extremely variable, usually of two awns, sometimes with one to several squamellae less than 0.5 mm. long.

[2] A specimen at Gray Herbarium (Parry in 1883!) from all Saint's Bay is annotated as the type by S. F. Blake but Gray cites the Belding specimen first and it was treated as the type by Watson (1929).

Distribution: west coast of Baja California from Sensal to Santa Margarita Island, chiefly on sand dunes. Apparently blooming throughout most of the year.

Although there is considerable variation present in this subspecies, I have found no logical basis for the taxonomic recognition of the variants. Two types stand out most conspicuously, one having nearly ovate leaves which are white and the second having more lanceolate or spathulate leaves which are grayish. Since this subspecies is allopatric with all other species, recent hybridization can be ruled out as a source of variability.

Until recently I had considered this taxon a species and a fairly good case could be made for continuing to do so. Artificial hybrids with the other subspecies are difficult to obtain. Attempts in four different years to secure hybrids with ssp. *canescens* either gave no seed or seed which failed to germinate. Plants secured from a cross of ssp. *niveus* as the female parent with ssp. *tephrodes* gave 2 plants with pollen fertility of 90 percent and three in the 50's. Meiosis examined in one of the latter plants was normal. These plants were very similar to the maternal parent; hence I am not absolutely sure that they are hybrids, although this species is normally self-incompatible. One plant was later obtained from a cross with ssp. *tephrodes* from California as the female parent which showed over 90% pollen stainability and was clearly a hybrid. Thus, although hybrids are fertile, it might be argued that the great difficulty in securing them indicates that these geographically separated races have reached full-fledged species level. In any event the subspecies designation serves to show the close realtionship of the three elements.

Hybrids of this subspecies have been secured with four perennials (*H. laciniatus, H. microcephalus, H. nuttallii, H. occidentalis*), all of which were highly sterile, although 17 pairs of chromosomes were observed in some cells. Attempts to obtain hybrids have failed with most of the other annuals, except *H. debilis* ssp. *debilis* and *H. praecox* ssp. *runyonii*. The latter gave two hybrids which showed 5% pollen stainability. Hybrids with *H. debilis* have been made on four occasions and pollen fertilities range from 20% to 88% with a mean of 61%. Examination of meiosis showed cells with both 17 bivalents and with 15 bivalents and a chain of four. An F_2 of four plants was obtained with pollen stainability ranging from 76 to 90%. The F_1 plants morphologically appear rather similar to *H. praecox* ssp. *praecox*.

This subspecies is the only member of the genus that is known to hybridize with species in all three sections of the genus, which raises the question as to whether ssp. *niveus* might be a "primitive" taxon or an element that has retained certain ancestral characteristics. Although its present geographical position does not seem a likely one for the origin of the genus, ssp. *niveus* does have certain morphological characteristics that might be "primitive." It is a tap-rooted perennial and such a species could have been the source of both the strict annuals and the perennials (Heiser, 1965). Secondly, it has some features of *Viguiera* which has been suggested as the ancestral stock for *Helianthus* (Heiser, 1957). Its general habit is rather similar to that of certain species of *Viguiera* and it frequently has pappus squamellae, also a characteristic of *Viguiera*.

It is conceivable that *H. debilis* ssp. *debilis*, although far removed geographically from *niveus* today, represents a type that early came out of the same gene pool as ssp. *niveus*; and through migration in opposite directions, the two reached their present areas at the far sides of the North American continent. This situation obviously recalls Matthew's (1915) hypothesis.

Although not mentioned in the description, attention should be called to the strong camphor-like odor of the leaves of this subspecies when crushed. So far as I am aware no other taxon in the genus shares this characteristic.

2b Helianthus niveus ssp. tephrodes (A. Gray), *stat. nov.*

H. tephrodes A. Gray in Torr. Bot. Mex. Bound. 90:1859. (T.: Colorado Desert of Calif., *Schott* 1855 GH!)

Viguiera tephrodes A. Gray, Proc. Amer. Acad. 17:218. 1882.
Viguiera nivea A. Gray in Brewer and Wats. Bot. Calif. 1:254. 1876.
Viguiera sonorae Rose and Standl. Contr. U. S. Nat. Herb. 16:20. t. 16. 1912.

Perennial or sometimes annual from stout tap root, erect or decumbent, 0.5-1.5 m. tall; stem appressed white sericeous-villous; leaves alternate above, deltoid or deltoid-ovate, entire or serrulate, 3.0-7.0 cm. long, 2.0-4.0 cm. broad, appressed white sericeous-villous, petiolate; phyllaries 2.5-4.0 mm. broad; lobes of the disk-corolla reddish-purple; achenes 4-8 mm. long, densely villous with long hairs; pappus of 2 (-3) long awns and several squamellae, the latter frequently over 0.5 mm. in length.
Distribution: Yuma Co. Arizona to Imperial Co., Calif. and western Sonora, Mexico. Mostly in sand hills. Sept.-May.

I have broadened my previous interpretation of this taxon (Heiser, 1955a) to include material from the Yuma area and western Sonora. This subspecies stands somewhat intermediate between the other two with some material from Arizona being transitional to ssp. *canescens* and that from Sonora approaching ssp. *niveus*. The size, pubescence, and pappus of the achenes of the material of this subspecies from California suggest a possible relationship with *H. anomalus*.

Artificial hybrids have been secured with the other two subspecies but natural hybrids are unknown.

2c Helianthus niveus ssp. canescens (A. Gray) *stat. nov.*

H. petiolaris var. *canescens* A. Gray, Smiths. Contr. Knowl. (Pl. Wright 1) 3:108. 1852. (T.: Texas, El Paso Co., *C. Wright 335*, GH!)
Gymnolomnia encelioides A. Gray, Proc. Amer. Acad. 19:4. 1884. (T.: Calif. San Diego Co., *Parish 1212* GH! Isotype MO, DS)
H. petiolaris var. *canus* Britton, Mem. Torrey Club 5:334. 1894.
H. canus (Britton) Wooton and Standley, Contr. U. S. Nat. Herb. 6:190. 1913.

Annual or rarely a perennial; stem usually erect to 1.5 m. tall, densely canescent, sometimes strigose near base; leaves lanceolate to ovate, entire to serrate, cuneate to subcordate, obtuse at apex, petiolate, to 12 cm. long and 6 cm. wide, densely grayish to silvery (rarely rusty) canescent with numerous fine, appressed hairs; peduncles long; disk 0.8-2.5 cm. in diam.; phyllaries usually slightly exceeding disk, 2-3 mm. broad, canescent or rarely strigose-canescent, usually drying dark green, erect or only slightly spreading; lobes of disk-corolla red to deep purple; pales 3-cuspidate, middle cusp long and acute, white-hispid with short hairs, sometimes conspicuously so in center of head; achene 3 (-4) mm. long, densely short villous; pappus of 2 awns, sometimes 1 or 2 smaller scales present.

Distribution: usually in sandy soils, southeastern New Mexico and western Texas west to southern California and northern Mexico, near sea level to 7500 feet. Blooming dates quite variable, usually late spring in California, mid to late summer in Texas and New Mexico.

This subspecies presents a somewhat anomalous situation with plants in the eastern part of the range appearing more similar to *H. petiolaris* than to the other two subspecies of *H. niveus*. In spite of this, however, there is justification for the present treatment. Although Waston (1929) treated this taxon as a species, Blake (1942) continued to recognize it as a variety of *H. petiolaris* as I did in my early work. Although there may be some intergradation with *H. petiolaris* in New Mexico, it is very distinct elsewhere. The dense-canescent pubescence usually serves as a good distinguishing characteristic, although occasional plants of *H. petiolaris* may crop up in various parts of its range more densely pubescent than normal. In addition, the pales are usually less densely pubescent than those of *H. petiolaris*; the leaves are usually broader, and more frequently serrate or serrulate; and the peduncles are longer. Hybridization might provide a possible explanation for the apparent intergradation in New Mexico, although I have found no hybrids in my field work in this area. It is also possible that the intergrading material represents types similar to those which may be the common ancestor of both *H. petiolaris* and ssp. *canescens*.

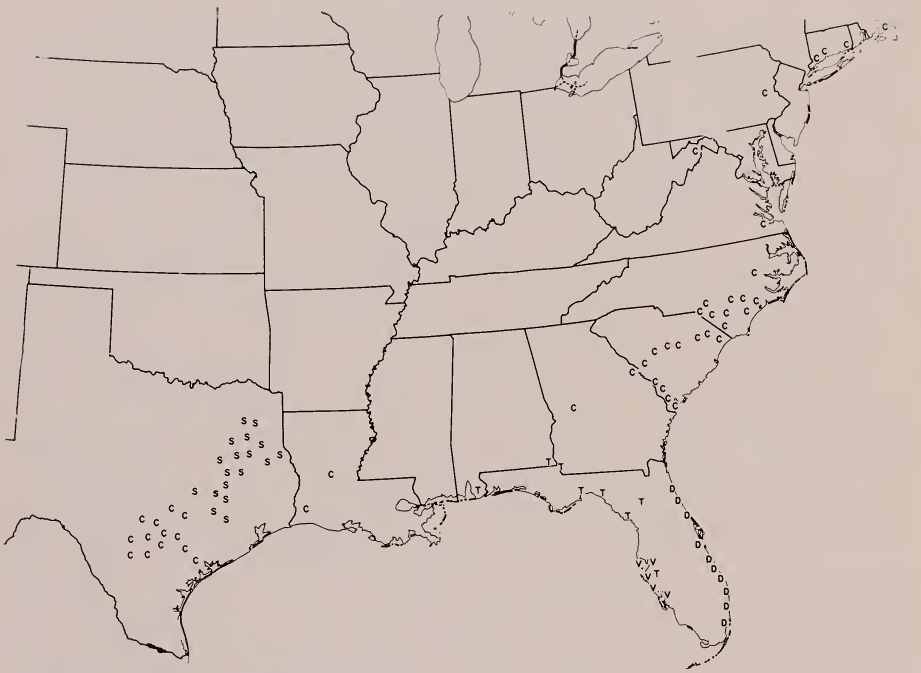
Two major morphological phases may be recognized within *H. niveus* ssp. *canescens*. Plants from Texas, New Mexico, and eastern Arizona which occur at fairly high elevation and bloom from late June to September, are rather tall, strict annuals, with large leaves, and rather densely pubescent pales, whereas plants from southwestern Arizona, from lower elevations and coming into bloom earlier, are erect or somewhat decumbent, tending to be short lived perennials with smaller leaves, sometimes somewhat fleshy, smaller heads and sparsely pubescent pales. These plants grade into subsp. *tephrodes* in certain features. The few samples from California, on the other hand, appear more nearly like some of those from the eastern part of the range but are not exact matches by any means. The California populations are in need of more study to determine their exact relationship to the other elements in the species.

Several crosses have been made within the subspecies utilizing two samples each from Arizona and Texas, and one sample from Sonora and New Mexico. Fertile hybrids are readily secured. The Texas sample when crossed with material of *H. niveus* ssp. *tephrodes* also gave fertile hybrids.

Artificial interspecific hybrids have been secured with several species. The hybrids with *H. angustifolius*, a perennial, were sterile. Those with *H. annuus*, *H. argophyllus*, *H. bolanderi*, *H. neglectus*, and *H. praecox* have very low fertility and display a very irregular meiosis with a maximum of 12 bivalents. Relatively few hybrids have been secured with subspecies of *H. petiolaris* inspite of several attempts. Somewhat surprisingly perhaps, the one secured with ssp. *petiolaris* showed higher fertility than those with ssp. *fallax*. Hybrids are fairly readily secured with *H. debilis* ssp. *debilis* and these regularly show 15 bivalents and a ring or chain of four chromosomes and have pollen fertilities averaging 22% (Heiser, 1961a, where this taxon is designated *H. canus*). Recently made hybrids have given the same results as those previously reported. Thus, although morphologically ssp. *canescens* is most similar to *H. petiolaris*, the chromosome structural arrangement appears more similar to that of *H. debilis*. As pointed out above, ssp. *niveus* also crosses readily with *H. debilis* ssp. *debilis*, producing hybrids somewhat more fertile than it produces with ssp. *canescens*.

3. **Helianthus debilis Nutt.** Am. Phil. Soc. n.s. 7:367. 1841. (T.: E. Fla. *Baldwin* BM; Photo, GH, US!)

Annual or short lived perennial; stem decumbent or erect to 2 m. tall, glabrous, hispid or hirsute, sometimes strongly purple mottled; leaves ovate, deltoid-ovate, to lance-ovate, usually dark green, cuneate to cordate, acute to acuminate at apex, nearly entire to deeply and irregularly serrate, nearly glabrous to hispid, or somewhat hirsute beneath, to 14 cm. long and 13 cm. wide, usually much smaller, petiolate; disk 1.0-2.2 cm. in diam.; phyllaries lanceolate, short acute to long attenuate, 1.5-3.0 mm. wide (sometimes wider in cultivated forms), glabrous or sparingly hispid to hispidulous; rays



Map 3. *Helianthus debilis.* C, ssp. *cucumerifolius*; D, ssp. *debilis*; S, ssp. *silvestris*; T, ssp. *tardiflorus*; V, ssp. *vestitus*

pale yellow to orange yellow, 11-20, 1.2-2.3 cm. long, 0.5-1.2 cm. wide (larger in cultivated forms); lobes of disk-corollas purple (rarely yellow in cultivated forms of ssp. *cucumerifolius*); pales 3-cuspidate, middle cusp acuminate, glabrous to hispid, rarely slightly villous; achenes 2.5-3.0 mm. long, sparingly pubescent to glabrous.

Chromosome number: n = 17

Key to Subspecies

Plants decumbent or nearly so; peduncles usually less than 20 cm. long; coastal regions of Florida

 Leaves serrulate or shallowly and regularly serrate; stems glabrous to hispid .... 3a *H. debilis* ssp. *debilis*

 Leaves rather deeply and irregularly serrate; stems hirsute ..... 3b *H. debilis* ssp. *vestitus*

Plants erect; peduncles usually over 20 cm. long; coastal and inland, Florida and Texas

 Lower leaves usually large, over 8 cm. long; peduncles very slender, 20-40 cm. long; disks relatively small, seldom over 1.5 cm. at anthesis; northeastern Texas, chiefly in oak-pine woods .... 3d *H. debilis* ssp. *silvestris*

 Lower leaves smaller, seldom over 9 cm. long; peduncles not conspicuously slender; disks 1.4-2.0 cm. broad at anthesis

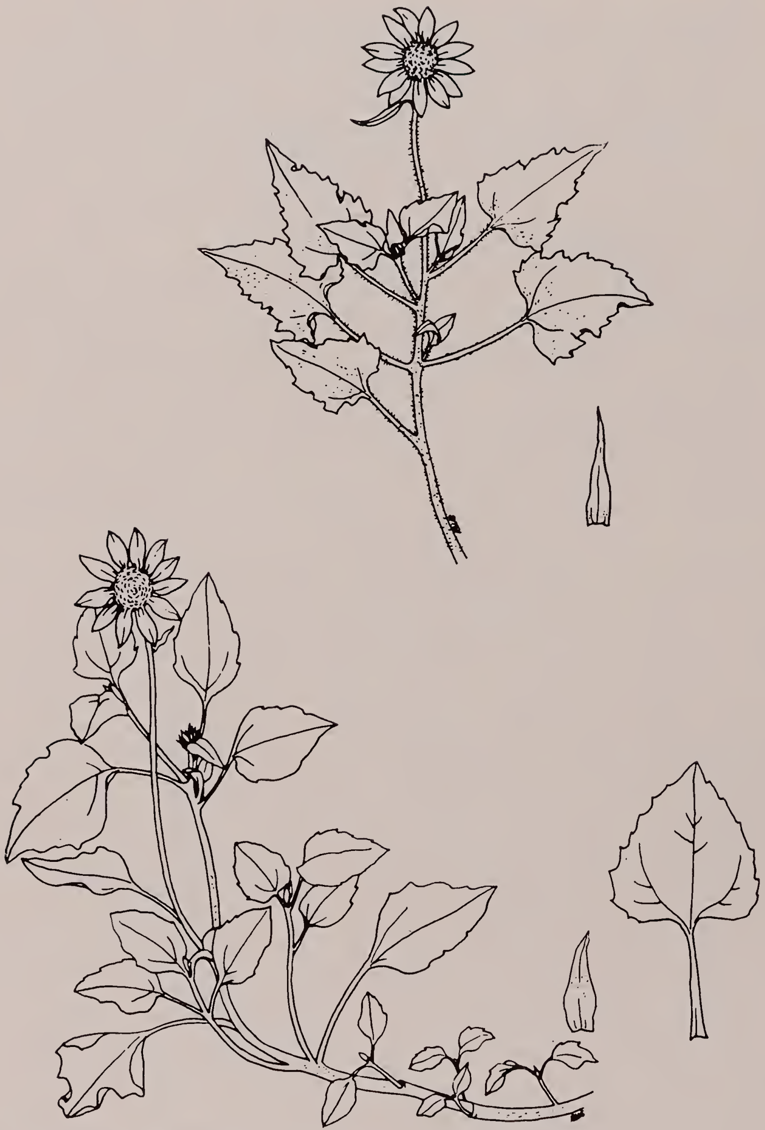


Fig. 3. *Helianthus debilis*; above, ssp. *vestitus*; below, ssp. *debilis*

Peduncles 25-50 cm. long; leaf usually shallowly, fairly regularly serrate; rays usually 2 cm. or more long; disks usually 1.6 or more in diameter at anthesis; south central Texas................................3e *H. debilis* ssp. *cucumerifolius*

Peduncles seldom over 25 cm. long; leaf usually deeply, irregularly serrate; rays usually less than 2 cm. long; west and north coastal Florida..3c *H. debilis* ssp. *tardiflorus*

3a H. debilis ssp. debilis

Annual or perennial, decumbent; stem and branches subglabrous to densely hispid; leaves irregularly shallowly serrate to nearly entire, glabrous to hispid, 3.0-10.0 cm. long, 2.0-8.0 cm. wide; peduncles generally 10-20 cm. long; disk 1.1 to 1.4 cm. in diameter at anthesis; phyllaries about 2 mm. wide, short-attenuate, sometimes squarrulose; rays 11-17, 1.2-2.0 cm. long, 0.5-1.0 cm. wide; central pales slightly hispid.

Distribution: East coastal Florida in sandy soil. Blooming throughout most of the year.

3b H. debilis ssp. vestitus (E. E. Wats.) Heiser, Madroño 13:154. 1956. (T. Fla., Pinellas Co. *Tracy 6919*, MSC!)

H. vestitus E. E. Wats. Pap. Mich. Acad. 9:347. 1929.

Annual or perennial, stem rather densely hirsute with whitish hairs, main stem erect or semi-erect to 30 cm. tall, lateral branches becoming decumbent; lower leaves deltoid-lanceolate to deltoid-ovate, usually cordate or truncate, rarely cuneate at base, irregularly serrate, occasionally somewhat undulate, 4.0-8.0 cm. long, 2.5-6.0 cm. wide; peduncles 9-15 cm. long, usually hirsute; disk 1.1-1.2 cm. in diam. at anthesis; phyllaries 1.5-2.0 mm. wide, short-attenuate; rays 12-15, 1.3-1.6 cm. long, 0.6-0.7 cm. broad; central pales hispid.

Distribution: Keys of central west Florida in sandy soil. Jan. to Oct.

3c H. debilis ssp. tardiflorus Heiser, Madroño 13:156. 1956. (T.: Fla., Sarasota Co. *Curtiss 1455*, MO!)

Erect annual usually much branched from near base, stems glabrous or sparingly hispid, 60-75 cm. tall; lower leaves wavy margined, 5-10 cm. long, 3-9 cm. wide, sub-cordate to cordate at base, deeply and irregularly serrate; peduncles 10-25 cm. long; disk diameter usually 1.4-1.5 cm.

Distribution: Isolated colonies chiefly on sandy beaches in western and northern Florida, also southwestern Georgia and southern Alabama. March-Sept.

3d H. debilis ssp. silvestris Heiser, Madroño 13:158. 1956. (T.: Texas, Nacogdoches Co. *Heiser 3086*, IND!)

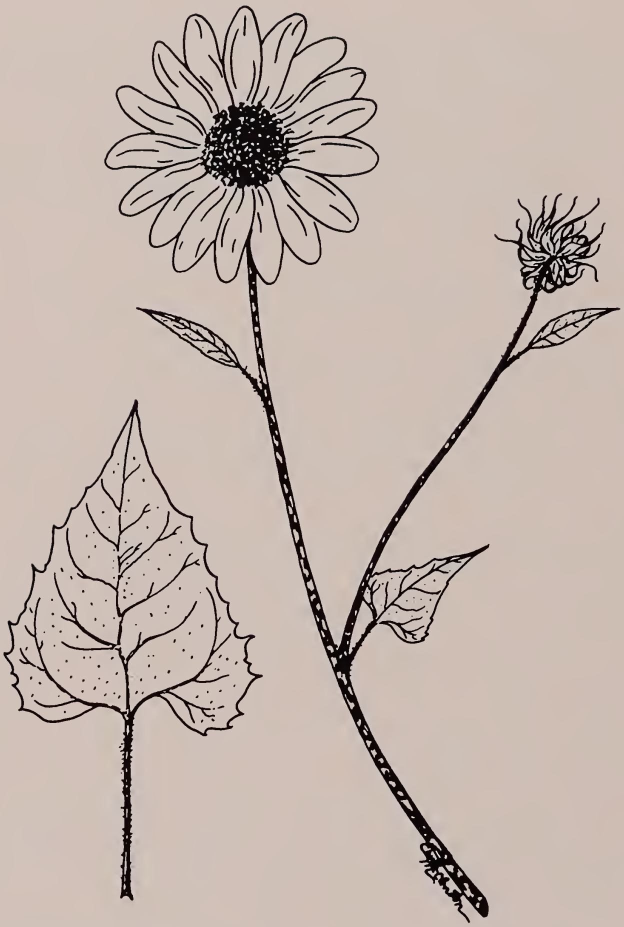


Fig. 3a. *Helianthus debilis* ssp. *cucumerifolius*

Erect annual, branches somewhat pendulous, branched mostly above, stems sparingly hispid to nearly glabrous, lower leaves 6-14 cm. long, 4-13 cm. wide, cordate at base, fairly regularly serrate; peduncles slender, 16-30 (-40) cm. long; disk diameter usually about 1.5 cm.

Distribution: Sandy soils in pine and oak regions of northeastern Texas. May to Oct. This subspecies grades into the next in the southern part of its range.

3e H. debilis ssp. cucumerifolius (T. & G.) Heiser, Madroño 13:160. 1956.

H. cucumerifolius Torrey & Gray, Fl. N. Am. 2:319. 1842. (T.: Texas, *Drummond 171*, NY!)
H. debilis var. *cucumerifolius* A. Gray, Syn Fl. 1^2:273. 1884.
H. debilis f. *cucumerifolius* Voss in Vilmorin, Blumengartn. (ed. 3) :482. 1894.

Annual, much branched, branches ascending, stem hispid below, usually conspicuously purple mottled, 55-65 cm. tall; lower leaves cuneate, truncate, or cordate at base, fairly regularly serrate, slightly wavy margined, 4.0-9.0 cm. long, 3.0-8.0 cm. wide; peduncles not conspicuously slender, 25-50 cm. long, disk 1.6-rarely 2.0 cm. in diam.; central pales of the chaff with hispid or slightly villous tips.

Distribution: In open sandy soils in southeastern Texas. April to Oct.

This species is one of the few in the genus which shows clear-cut differentiation into geographical races. On morphological grounds *H. debilis* ssp. *debilis* and ssp. *vestitus* might well be considered species as was done by Watson (1929), for they are certainly as well differentiated from each other as are many of the perennials. The other three subspecies are fairly similar and are sometimes difficult to distinguish in herbarium material. The subspecies are for the most part allopatric and all produce fertile artificial F_1 hybrids with each other.

While there is little evidence to suggest which of the subspecies is the most "primitive," it might be logical to assume that the decumbent subspecies are derived. Both of them are found at the periphery of the range. However, the greater ease with which *H. debilis* ssp. *debilis* crosses with *H. niveus* suggests to me the possibility that ssp. *debilis* is the oldest race and has migrated to the periphery of the range and has been replaced by other subspecies along the way (see discussion under *H. niveus*).

The relationship of this species, both morphologically and on the basis of hybridization studies, is clearly with *H. praecox*. In an earlier paper (Heiser, 1956) *H. praecox* was treated as part of this species, chiefly because of the difficulty of distinguishing *H. debilis* ssp. *cucumerifolius* from *H. praecox* ssp. *runyonii* in southern Texas. However, since most of the species may show some intergradation in zones of contact this is not now considered sufficient reason for combining the two taxa. The two species always give hybrids with reduced fertility and one ring or chain of four chromosomes and occasionally more are seen at meiosis in the F_1. Moreover, the generally broader, shorter phyllaries, the tendency for the leaves to be more constricted in the middle, and the more pubescent pales of *H. praecox* are fairly reliable in separating the two.

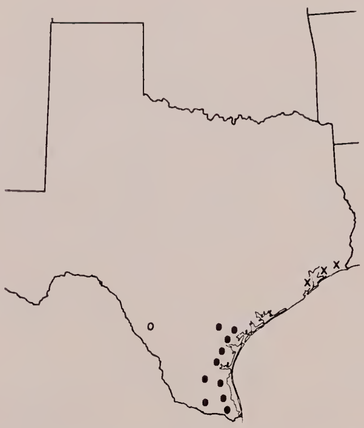
The Florida subspecies of *H. debilis* are geographically separated from closely related species and are remarkably "pure" for this genus. In Texas the subspecies are known to hybridize with *H. annuus* (Heiser, 1951b) and some introgression is thought to occur. It is also likely that hybridization between *H. debilis* ssp. *cucumerifolius* with *H. praecox* ssp. *runyonii* occurs which makes it difficult to identify certain specimens from southern Texas. So far as is known, this species does not meet *H. petiolaris* in Texas; but hybridization in the Dallas area, where they come the closest together, should be looked for as well as in South Carolina where both are introduced.

Artificial hybrids have been secured with several other annual species (*H. annuus*, *H. anomalus*, *H. argophyllus*, *H. bolanderi*, *H. neglectus*, *H. niveus*, *H. petiolaris*, and *H. praecox*). These hybrids generally show very low fertility with the highest being secured in crosses with *H. praecox*. Rather highly sterile hybrids were secured with one perennial, *H. floridanus*.

Weeds and ornamentals.—*Helianthus debilis* has been reported as an introduction in several eastern and southern states (Heiser, 1956). These weedy forms, for the most part, appear rather similar to *H. debilis* ssp. *cucumerifolius* and can be referred to this subspecies. This species has also been fairly extensively cultivated and is handled by a number of seed companies. It is a more graceful plant than *H. annuus* and perhaps the best annual in the genus for ornamental purposes. The cultivated races seem to have been derived mainly from *H. debilis* ssp. *cucumerifolius* but frequently have larger disks, more numerous rays, and broader phyllaries. A number of color variants are known with rays ranging from primose to a wine red, and the disk flowers may be either yellow or deep purple. Many of the variants probably arose as the result of mutation but hybridization with ornamental forms of *H. annuus* may also be involved.

4. Helianthus praecox Engelm. and Gray, Boston Jour. Nat. Hist. 5:221. 1847. (T.: Texas, Galveston Co., *Lindheimer 97*, MO!)

Annual; stem erect or becoming somewhat procumbent to 1.5 m. tall, hispid to hirsute, purple-mottled or straw colored; leaves deltoid-ovate, usually with slight constriction near middle, cuneate to subcordate, acumi-



Map. 4. *Helianthus praecox.* X, ssp. *praecox*; O, ssp. *hirtus*; solid dots, ssp. *runyonii*

nate, frequently grayish green, hispid to sparingly hirsute, serrulate or shallowly serrate with sharp teeth, blade to 9 cm. long and 7 cm. wide, petiolate; peduncles 15-40 cm. long; disk 1.3-1.8 cm. in diam.; phyllaries broadly lanceolate, short acute, 3-4 mm. wide, hispidulous to sparingly hispid-hirsute; rays 11-16, 1.7-2.7 cm. long, .7-1.2 cm. wide; disk-flowers purple; pales 3-cuspidate, middle cusp short acuminate, hispid to short-villous; achene 2.5-3.0 mm. long, lightly villous to nearly glabrous.

Chromosome number: n = 17

Key to Subspecies

Plants procumbent or erect with branches horizontal; stems not densely hispid-hirsute; tips of central pales of the chaff seldom villous; Galveston Island and adjacent mainland, Texas .... 4a *H. praecox* ssp. *praecox*

Plants erect with ascending branches; tips of central pales of the chaff usually villous

  Stems hirsute but not densely so; peduncles seldom longer than 30 cm.; leaves seldom longer than 8 cm.; rays usually fewer than 14; southern Texas .... 4b *H. praecox* ssp. *runyonii*

  Stems densely hirsute or hispid-hirsute; peduncles usually 30-40 cm. long; leaves frequently 8-9 cm. long; rays usually 14 or more; Carrizo Springs, Texas .... 4c *H. praecox* ssp. *hirtus*

4a Helianthus praecox ssp. praecox

H. debilis var. *praecox* A. Gray in Torr., Emory, Rep. U.S.-Mex. Bound. (Bot.), 90. 1859.

H. debilis ssp. *praecox* Heiser, Madroño, 13:160. 1956.

Usually somewhat procumbent, occasionally erect with horizontal branches, to 40-50 cm. tall; stem hispid to hirsute; leaves 3.0-8.0 cm. long.

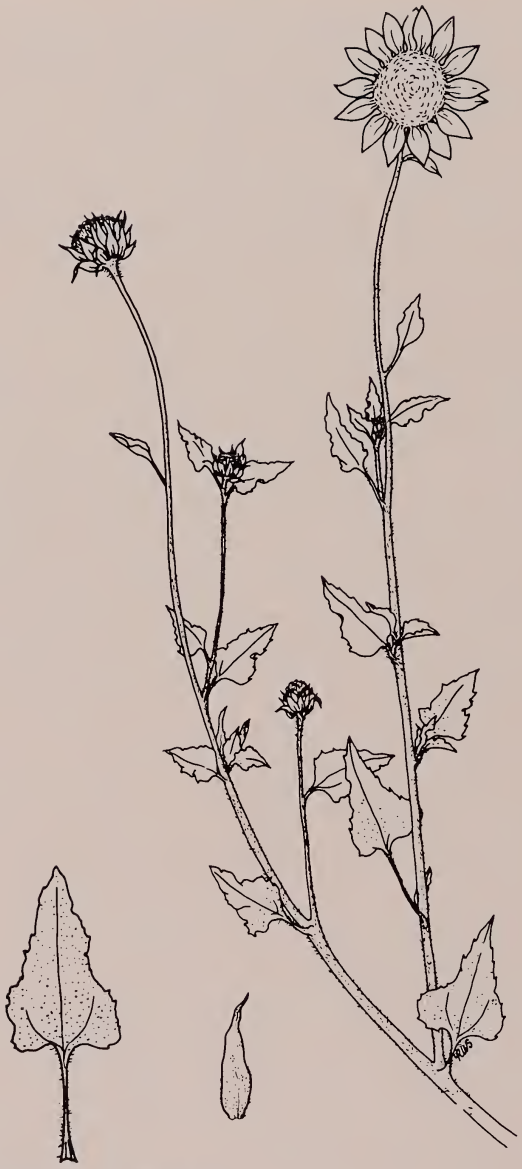


Fig. 4. *Helianthus praecox* ssp. *runyonii*

2.0-7.0 cm. wide; peduncles 15-30 cm. long; disk ca. 1.4 cm. in diam.; rays generally 14-15; central pales of the chaff hispid to slightly villous.

Distribution: Sand, Galveston Island, Texas and adjacent mainland. June-Nov.

The procumbent condition of this species appears to be an adaptation to its coastal existence and appears to represent an independent parallel development of that which occurred in *H. debilis.* Superficially this subspecies is rather similar to *H. debilis* ssp. *vestitus*, although not so densely pubescent.

4b Helianthus praecox ssp. runyonii, *stat. nov.*

H. debilis ssp. *runyonii* Heiser, Madroño, 13:161. 1956. (T.: Texas. Willacy Co., *Runyon 4365* IND!)

Plants erect, stems hispid or somewhat hispid-hirsute, 50-60 cm. tall; leaf blades 3.0-7.5 cm. long, 2.0-6.0 cm. wide; peduncles 20-30 cm. long; disk ca. 1.4 cm. in diameter; rays generally 11-13; central pales of the chaff villous.

Distribution: Coastal "prairies" in southern Texas, April-Nov.

This subspecies appears to intergrade with *H. debilis* ssp. *cucumerifolius* and certain herbarium specimens are difficult to identify precisely as to one or the other.

4c Helianthus praecox ssp. hirtus, *stat. nov.*

H. debilis ssp. *hirtus* Heiser, Madroño 13:162.1956 (T.: Texas, Dimmit Co., *Heiser 3064*, IND!)

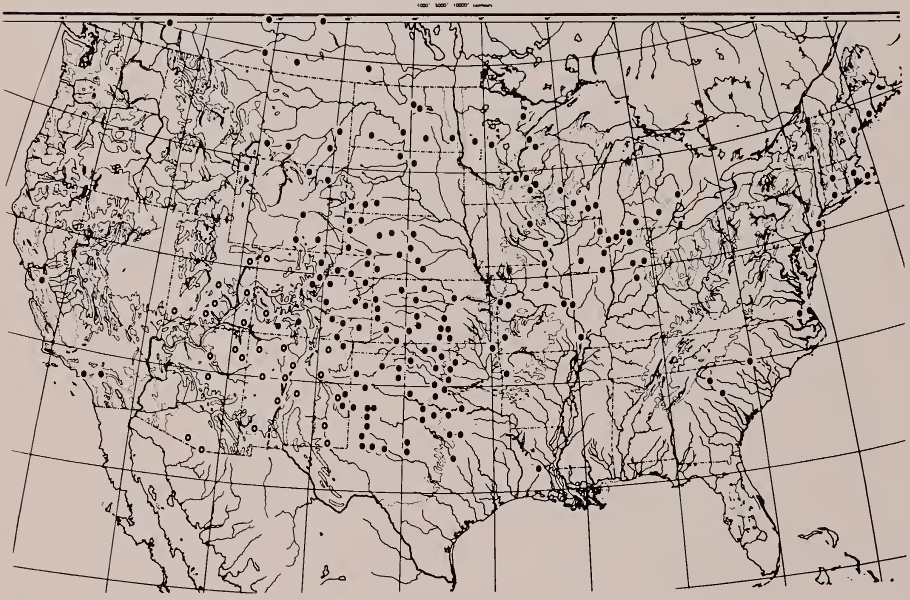
Plants erect, stems hispid-hirsute, usually densely so below, 50-60 cm. tall, leaves 3.0-9.0 cm. long, 2.0-7.0 cm. wide; peduncles 30-40 cm. long; disk usually over 1.5 cm. in diam.; rays 14-16; central pales of the chaff villous.

Distribution: Known only from area of Carrizo Springs, Dimmit Co.; Texas (*Schott 561* from "Rio Bravo del Norte" may belong to this race.) This highly endemic subspecies is rather similar to the previous except in pubescence but seems to be well isolated from it geographically.

Both on morphological grounds and on the basis of chromosome behavior in hybrids, this species appears closely related to *H. debilis* and *H. petiolaris*; in fact, in many ways it is somewhat intermediate between them. On basis of chromosome pairing it also appears closely related to *H. neglectus.* Artificial hybrids of this species have also been secured with *H. annuus, H. argophyllus, H. bolanderi* and *H. niveus.* The three subspecies of *H. praecox* have been crossed in all possible combinations and give fertile hybrids (Heiser, 1956).

Natural hybrids are known between *H. praecox* subsp. *hirtus* and *H. annuus* (Heiser 1951b, where this subspecies is included under *H. debilis* var. *cucumerifolius*). Hybrids also probably occur between *H. praecox* ssp. *runyonii* and *H. debilis* ssp. *cucumerifolius*, and hybrids of this subspecies with *H. argophyllus* should be sought in southern coastal Texas.

5. Helianthus petiolaris Nutt. Jour. Acad. Sci. Phil. 2:115. 1821.
(T.: "Banks of the Arkansas," Okla.? *Nuttall*, BM, Photo US!)



Map 5. *Helianthus petiolaris.* Solid dots, ssp. *petiolaris*, open dots, ssp. *fallax*

Annual 0.4-2.0 m. tall, usually much branched; stems hispid or strigose to hispidulous or nearly glabrous; leaves deltoid-ovate, deltoid-lanceolate to lanceolate, entire to shallowly serrate or obscurely serrate, cuneate to truncate at base, 4.0-15.0 cm. long, 1.0-8.0 cm. wide, strigose on both surfaces, frequently bluish-green in color, petiolate; peduncles 5-40 cm. long; disks 1.0-2.4 cm. in diam.; phyllaries lanceolate to ovate-lanceolate, hispidulous on backs, rarely slightly hirsute to nearly glabrous, short ciliate or glabrous on margins, 2.0-4.5 (-5.5) mm. wide; middle cusp of chaff slightly exceeding disk-flowers, those in center of head densely long white ciliate or hirsute at apex; disk flowers reddish-purple, very rarely yellow; achenes lightly villous, 3.5-4.5 mm. long; pappus of 2 awns.

Chromosome number: n = 17.

Key to Subspecies

Phyllaries generally 3.0-5.0 mm. wide; lower leaves usually about twice as long as broad; peduncles usually naked; stem hispidulous to strigulose . . . . 5a *H. petiolaris* ssp. *petiolaris*

Phyllaries generally 2.0-3.5 mm. wide; lower leaves usually more than twice as long as broad; peduncles usually with leafy bract subtending head; stem usually somewhat hispid . . . . 5b *H. petiolaris* ssp. *fallax*

5a Helianthus petiolaris ssp. petiolaris

H. patens Lehm. Ind. Sem. Hort, Hamb., 8. 1828.
H. petiolaris var. *humilis* Nees in Neuwied., Reise N. Am. 2:441. 1841.
H. integrifolius Nutt. Trans. Amer. Phil. Soc., II, 7:336. 1841.
H. integrifolius var. *gracilis* Nutt., l.c.
H. petiolaris var. *patens* Rydb. Mem. Torrey Club 5:334. 1894.
H. petiolaris var. *phenax* Ckll. Nature 66:174. 1902.
H. petiolaris integrifolius Ckll. Torreya 18:13. 1918.

Stems usually not exceeding 1.4 m., usually green, rarely red, pubescent with slender appressed hairs, branching usually near base; lower leaves usually deltoid-ovate to oblong lanceolate; peduncles relatively short; phyllaries 18-45, mostly ovate-lanceolate or oblong-lanceolate, 10-14 mm. long; rays 15-30; anthers generally purple, rarely red.

Distribution: Mostly in sandy soil, Great Plains east of the Rocky Mountains, southern Canada to northern Texas; an introduced weed in California and eastern United States. Sea level to 5000 ft. June-Sept.

It is probable that all the synonyms listed here belong to this subspecies but types have not been seen, and it is conceivable that some might better be referred to the next subspecies. Cockerell's observations were made near Boulder, Colorado where either one of the subspecies might be found.

5b Helianthus petiolaris ssp. fallax Heiser, Rhodora 60:279. 1958. (T.: Ariz. Apache Co., *Heiser 4149* IND!)

Stems to 2 m., red or green, pubescent with slender appressed hairs and usually longer spreading thick based trichomes; branching mostly in upper part; lower leaves lanceolate to deltoid-lanceolate; peduncles short to long; phyllaries 14-30, mostly oblong-lanceolate to lanceolate, 12-20 mm. long; rays 10-20; anthers generally red, rarely purple.

Distribution: Western Colorado to Utah south to New Mexico and Arizona, 4000-8000 feet. June to Sept.

This species has been the subject of a detailed morphological and cytological study (Heiser, 1961a). Three cytological races are recognized: group A apparently comprising most populations referred to *H. petiolaris* ssp. *petiolaris*; group B comprising all of ssp. *fallax* so far as is known and certain

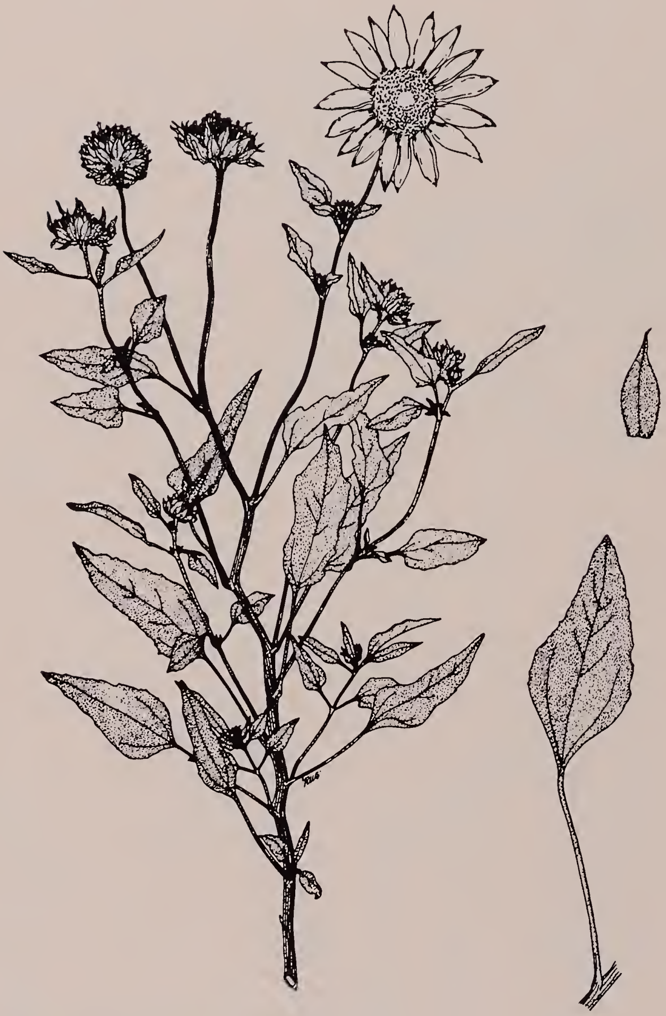


Fig. 5a. *Helianthus petiolaris* ssp. *petiolaris*

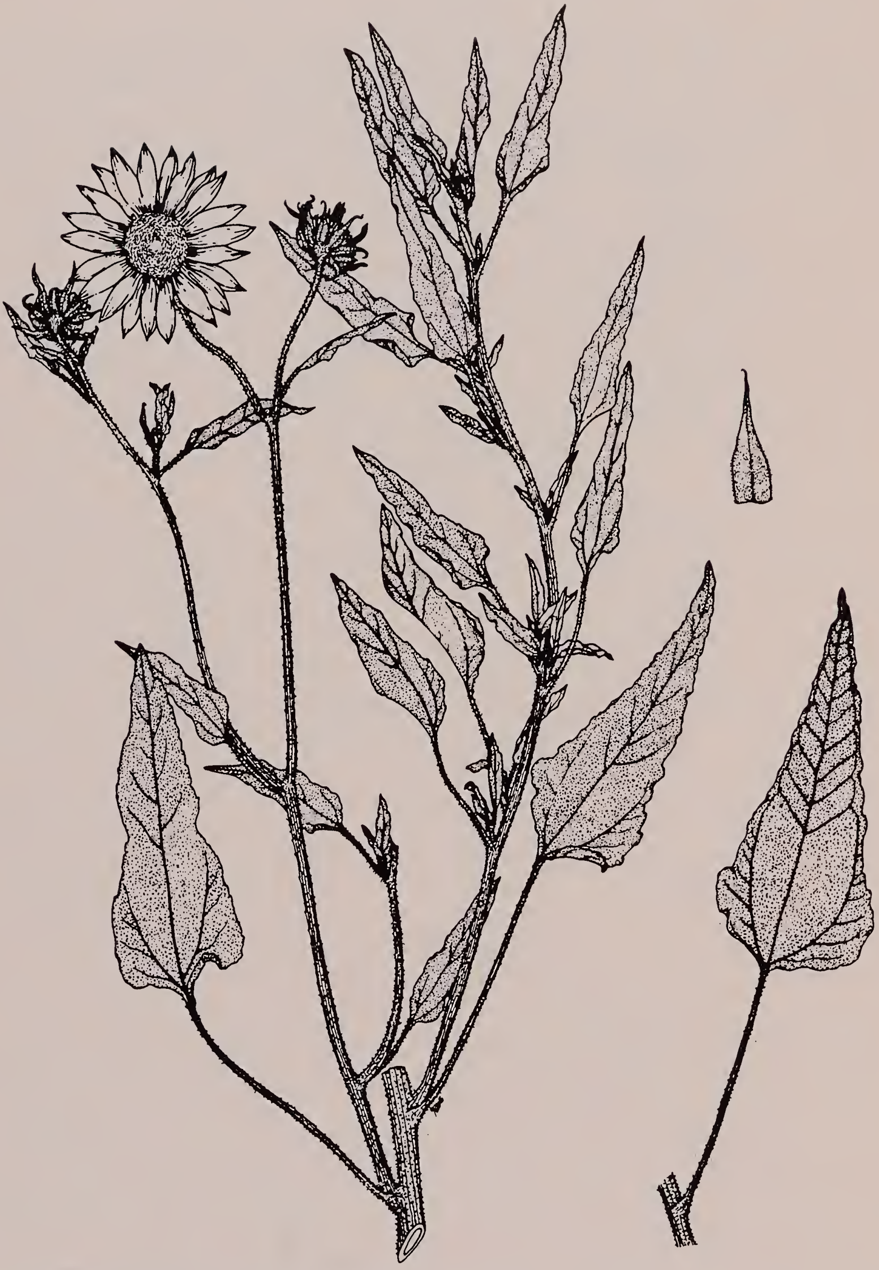
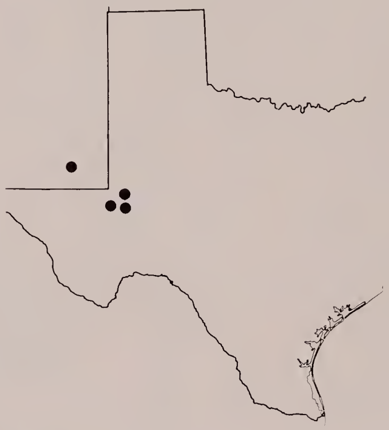


Fig. 5b. *Helianthus petiolaris* ssp. *fallax*

southern populations of ssp. *petiolaris*; and group C consisting of a single population from Minnesota referred to ssp. *petiolaris.* Hybrids within members of any cytological race are fertile, whereas hybrids between the groups show some reduction in fertility. The implications of this are discussed in the paper cited above.

Artificial hybrids of *H. petiolaris* have been secured with *H. annuus*, *H. argophyllus*, *H. bolanderi*, *H. debilis*, *H. neglectus*, *H. niveus* and *H. praecox*. Although attempts have been made to secure hybrids with a number of diploid perennials, none has resulted in seed. Natural hybrids are known with *H. annuus* and hybrids are to be expected wherever the ranges of these two species overlap. The possibility of natural hybridization with *H. niveus* ssp. *canescens* and *H. debilis* is discussed under those taxa.

6. Helianthus neglectus Heiser, Rhodora 60:275. 1958. (T.: Ector Co., Texas. *Heiser 4123,* IND!)



Map 6. *Helianthus neglectus*

Annual, 0.8-2.0 m. tall, usually much branched; stem densely hispid to hispid-hirsute below, hispid to nearly glabrous above; lower leaves ovate, cordate or rarely truncate, subentire or remotely serrulate, 7-14 cm. long, 7.5-12.3 cm. wide, petioles nearly as long as leaves; peduncles 10-40 cm. long, phyllaries 25-35, lanceolate, long attenuate, 2.5-4.0 cm. broad; disk ca. 2.3-2.8 cm. in diameter; rays 21-31, 3.0-3.9 cm. long, 1.0-1.4 cm. wide; pales 3-cuspidate, middle cusps in center of the disk white hirsute; achene ca. 4 mm. long, with short appressed hairs, becoming glabrous.

Distribution: sandy soils, southeastern New Mexico and adjacent Texas. July-Sept.

This species is limited, so far as is known, to the area surrounding Monahans, Texas and to a population extending from the Mescalero Ridge east to

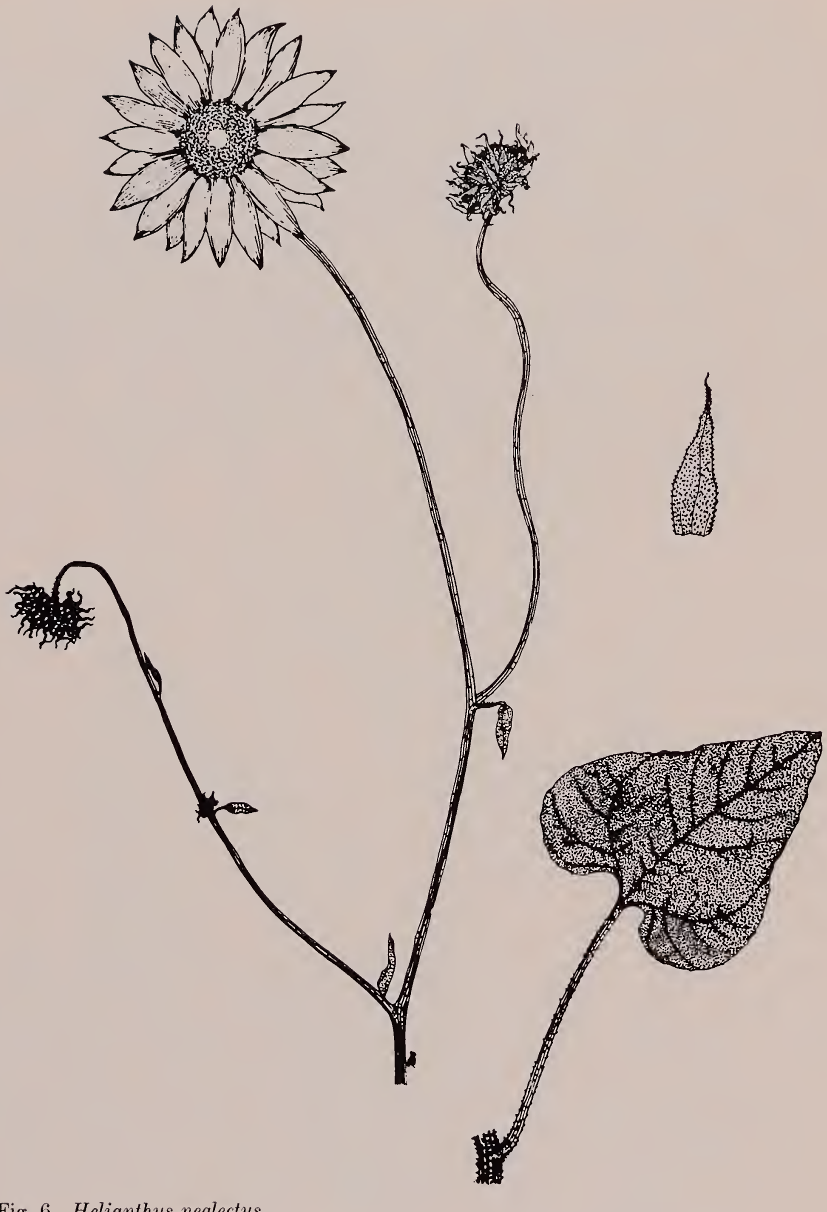


Fig. 6. *Helianthus neglectus*

Artesia in New Mexico. In the latter area it was abundant along a stretch of Highway 83 for over 30 miles where it was the only sunflower observed.

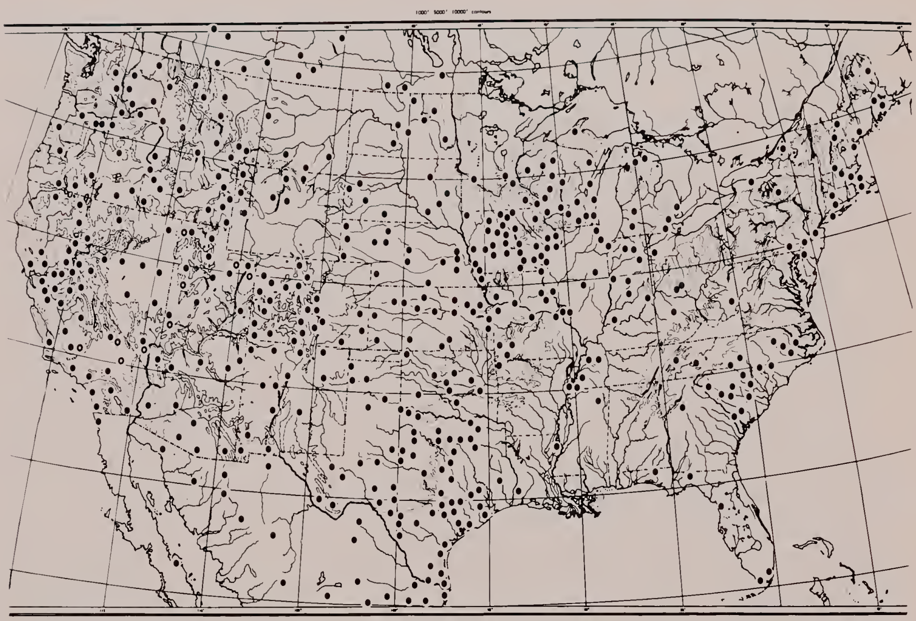
In the original description the possibility of a hybrid origin for this species from *H. annuus* x *H. petiolaris* was mentioned. *Helianthus neglectus* differs from *H. petiolaris* by a single translocation, and morphologically shows close similarity to this species in leaf color, leaf margin, phyllary shape, and pale pubescence, and ecologically in its restriction to sandy soils. It differs from *H. annuus* by several translocations; but in leaf shape, phyllary attenuation, number of phyllaries, and in ray number and ray size, it is similar to *H. annuus*. The stem and leaf pubescence and the size of most of the characters are somewhat intermediate between these two species. Its most unique feature is the very long peduncles which have a tendency to come off at an angle greater than 45° while in most other species the angle is less than 45°. Since *H. annuus* and *H. petiolaris* are known to hybridize in many areas, it seems possible that such hybridization could have given rise to a stable, fertile type in a manner suggested by Grant (1963). The unique features could have developed by mutation subsequent to the formation of the species or through the interaction of genes from the parental species. On the other hand, an origin by some other manner might be postulated. For example, the morphological similarity of *H. neglectus* to two other species might be explained by assuming that *H. neglectus* is the ancestral type which gave rise to *H. annuus* and *H. petiolaris*, or that all three species developed from a common ancestor. The fact that there is also a slight disjunction in the range of the species between the New Mexican colony and the Texas population might be used as an argument against an origin through hybridization.

The fertility and cytology of artificial hybrids of *H. neglectus* with *H. annuus*, *H. debilis*, *H. niveus*, *H. petiolaris* and *H. praecox* are summarized in the original account of this species. Since that time hybrids have been secured with *H. argophyllus*, which like the others listed above show considerable reduction in fertility. Plants that appear to be natural hybrids with *H. petiolaris* have been seen 20 miles west of Monahans, but no herbarium specimens were made.

Gray (1884) mentions that "*H. neglectus*, Otto, in Berlin Garden is either a glabrous form of *H. strumosus*, or is *H. laevigatus*." Since Otto's name was never validly published it has no standing.

7. **Helianthus annuus L.** Sp. Pl. 906. 1753. (T.: LH, Photo. GH!)

H. indicus L. Mant. 1:114. 1761.
H. tubaeformis Nutt. Gen. N. Am., 2:177. 1818. (not Jacq.)
H. platycephalus Cass. Dict. Sci. Nat. 22:352. 1821.



Map 7. *Helianthus annuus*. The distribution of G ("jaegeri") is shown by open dots

H. macrocarpus DC. Pl. Rar. Jard. Gen. Vme, Not., 8. 1826.
H. annuus var. *macrocarpus* Ckll. Science 40:709. 1914.
H. ovatus Lehm. Ind. Sem. Hort. Hamb., 16. 1828
H. lenticularis Dougl. Bot. Reg., t. 1265. 1829.
H. annuus lenticularis Ckll. Bot. Gaz. 45:338. 1908.
H. annuus ssp. *lenticularis* Ckll., Science 40:284. 1914.
H. annuus var. *lenticularis* Steyerm. Rhodora 62:132. 1960.
H. annuus f. *lenticularis* Boivin, Nat. Canad. 87:35. 1960.
H. colossus Kunze, Otto & Dietr. Allg. Gartenz. 6:43. 1839.
H. erthrocarpus Barth. Linnaea 14. Litt. 125. 1840.
H. multiflorus Hook. Fl. Bor. Am. 1:313. 1840. (not L.)
H. grandiflorus Wender ex Stend. Nom., ed. 2, 1:737. 1841. (not Juss.)
H. lindheimerianus Scheele, Linnaea 22:159. 1849. (T.: Texas, *Lindheimer 259* MO!)
H. cirrhoides Lehm. Hamb. Gart. Zeit. 8:458. 1852. (*fide* Blake, Contr. U.S.N.H. 26:253. 1930)
H. aridus Rydb. Bull. Torrey Club 32:127. 1905. (? see Heiser, 1948)
H. annuus lenticularis var. *aridus* Ckll. Am. Nat. 49:611. 1915.
H. jaegeri Heiser, Bull. Torrey Club 75:513. 1948. (T.: Calif. San Bernardino Co., *Jaeger*, POM #270144!)
H. annuus ssp. *jaegeri* Heiser, Contr. Dudley Herb. 4:317. 1955.

H. annuus ssp. *texanus* Heiser, Am. Midl. Nat. 51:299. 1954. (T.: Texas, Uvalde Co., *Heiser 3062*, IND!)
H. annuus var. *texanus* Shinners, Sida 1:377. 1964.
H. annus (*sic*) f. *fallax* Boivin, Nat. Canad. 87:35. 1960.

Annual, 1.0-3.0 m. tall, unbranched to much branched, stem usually hispid; leaves mostly alternate, ovate-lanceolate to ovate, conspicuously serrate, lower-most leaves cordate to subcordate, usually hispid both surfaces, 10-40 cm. long, 5-35 cm. wide, long petiolate; disk (1.5-) 2.0 cm. in diam. or usually much larger; phyllaries ovate or ovate-lanceolate, abruptly attenuate, hirsute, hispid, or rarely glabrous on backs, usually ciliate on margin, (3-) 5 mm. or more broad; rays 17 or more, rarely fewer, usually 2.5 cm. or more long; lobes of disk-corollas reddish or purplish, occasionally yellow; pales deeply 3-cuspidate, middle cusp attenuate, hispid or rarely glabrous near apex; achenes (3.0) -5.0-(15.0) mm. ong, glabrate, variously colored; pappus scales usually two, extra scales sometimes present, particularly in cultivated forms.

Chromosome number: n = 17

Distribution: Throughout the United States with the greatest concentration east of the Mississippi, extending into Canada and Mexico. Late July-Sept.

The map has been compiled solely from uncultivated specimens seen by the author. The distribution of this species in western North America is probably more extensive than indicated and it probably occurs in every county in many of the states. The distribution in the east is also probably greater than the map shows but in that region it seldom forms the large populations characteristic of the west and in all probability many of the specimens represent escapes from cultivation.

In all probability the synonymy is not complete. Certain names for this species are found in the Russian literature (Ventslavovich, 1941) which have never been validly published. The plant which has been considered the type of this species has been discussed elsewhere (Heiser, 1949). At that time it was thought that it represented the weed sunflower, but it could be a hybrid of the cultivated monocephalic sunflower and a wild or weedy representative of the species. Fortunately, there is no question that the sunflower on which Linnaeus based the name is *H. annuus* as now interpreted. This species has probably been studied more intensively than any of the others by both the writer (Heiser, 1954) and others but it still presents many problems. Part of the difficulties stems from the fact that it is widely distributed, comprises both weeds and cultivated plants, and hybridizes naturally with several other species. With the possible exception of *H. strumosus*, as here interpreted, it is the most variable species in the genus, but unlike that

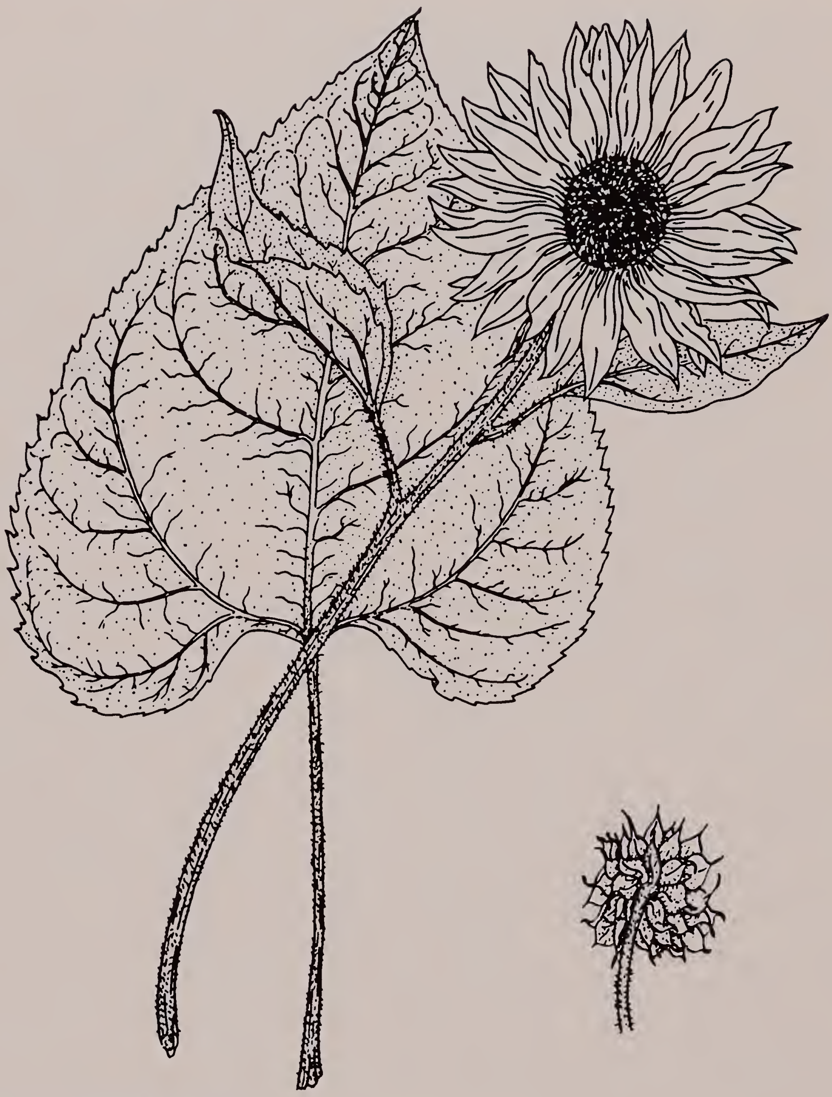


Fig. 7. *Helianthus annuus*

"species" it appears to be a "natural entity"; in all probability it is monophyletic whereas *H. strumosus* may be polyphyletic.

In an earlier publication (Heiser, 1954) four infraspecific taxa were recognized in this species and a fifth (Heiser, 1955a) was added later. Although this classification served to call attention to some of the principal variants within the species, it is now realized that it is both an unnatural and unrealistic treatment. Partly because of the inadequacy of many herbarium specimens and partly because of extensive intergradation it is often difficult to identify specimens precisely as to subspecies. Therefore, in the present work a less formal treatment is being adopted.

Key to "forms" of *H. annuus*

- Plants cultivated
  - Usually monocephalic; phyllaries over 8.5 mm. broad; rays orange-yellow ..... A
  - Usually polycephalic; phyllaries 6-9 mm. broad; rays orange-yellow, primose, or with red pigmentation ..... B
- Plants uncultivated
  - Phyllaries 3-4 mm. broad, glabrous or hispidulous; disks 1.5-2.0 cm. in diameter ..... G
  - Phyllaries usually over 3.5 mm. broad, conspicuously ciliate on margins, glabrous to densely pubescent on backs; disks usually over 2.0 cm. in diam.
    - Disk 3.0-5.0 cm. in diameter; rays of terminal head usually more than 25; central and eastern North America
      - Plants to 3 m. tall; chiefly in rural areas ..... D
      - Plants generally 1.7-2.2 m. tall; chiefly in industrial areas C
    - Disk generally 2.0-3.0 cm.; rays of terminal head 15-25; Texas and western North America
      - Phyllaries usually densely hirsute on backs; plants 0.5-1.5 m. tall; primarily in Rocky Mountains ..... F
      - Phyllaries merely hispid or sparingly hirsute; plants generally 0.8-2.2 m. tall
        - Rays light orange-yellow; leaves frequently somewhat deeply and and irregularly serrate ..... E
        - Rays deep orange-yellow; leaves more shallowly and regularly serrate ..... H

CULTIVATED PLANTS

A. *Cultivated for seed or fodder.* The giant monocephalic sunflowers can be referred to *H. annuus* var. *macrocarpus* (DC.) Ckll. if a formal designation is desired; "*H. cultus*" is generally employed in the Soviet. Numerous cultivars are known of which the Russian Mammoth is most common in the United States. Numerous "proles" have been described in the Soviet (Ventslavovich, 1941) and the North American Indian varieties are treated by Heiser (1951c). Two of the latter, the Hopi sunflower of Arizona and *maiz negro* or *maiz de tejas* of Mexico, are quite distinctive, probably reflecting genetic differentiation during long isolation from other varieties. The cultivated sunflower is clearly North American in origin (Heiser, 1955b). A summary of the breeding work with this sunflower may be found in Rudorf (1961).

B. *Cultivated for ornament.* In an earlier treatment (Heiser, 1954) the ornamentals were referred to *H. annuus* subsp. *annuus.* They differ from the wild sunflowers chiefly in the number or the color of the rays—primrose, chestnut, plum—and their sometimes larger disk and achenes. The red-rayed forms are apparently all derived from a mutant plant found in the wild in Colorado by Mrs. T. D. A. Cockerell (Cockerell, 1912, 1918). The "double-flowered" forms probably originated in Europe shortly after the introduction of the sunflower there. Cockerell (see Watson, 1929, p. 361) has given formal taxonomic recognition to many of the ornamental variants, but there seems little to be gained by trying to designate the various ornamental forms with Latin names.

UNCULTIVATED PLANTS

The wild and weedy members of this species show great variation and it seems impossible at present to arrive at a satisfactory classification. Hence, some of the major morphological types which seem to have some correlation with geographical distribution will be listed. The spread of these plants by man from one part of the country to another as well as occasional hybridization with cultivated *H. annuus* and other species probably largely explains the lack of clearly defined races in this species. Although a great deal of environmental modification of the phenotype is known for this species, the classes listed below reflect differences which are maintained when grown in the experimental garden. The name "*H. ruderalis*" is employed in recent Russian literature for the wild form of *H. annuus.*

C. In the central and to a lesser extent in the eastern United States, sunflowers are common around larger cities and differ somewhat from the rural types. Possibly tolerance to smoke may account for the success of this sunflower in industrial areas. It would be most interesting to have detailed ecological comparisons of this sunflower with other types. It is also possible that this sunflower represents the perpetuation of a transitional stage in the development of the cultivated sunflower and was originally an Indian camp follower which moved into its present areas within the last few hundered years. It should also be noted that hybrids of the various types listed below when crossed with the cultivated sunflower (A), produce plants rather similar to plants which are found occurring naturally around St. Louis and Indianapolis (Heiser, 1965b).

D. The common weed along roadsides and in cultivated fields in Missouri, eastern Kansas, Nebraska, portions of Iowa and perhaps elsewhere is generally taller, reaching four meters, and more branched than the previous.

E. In eastern Texas there is a high frequency of plants with light yellow-orange rays, strongly purple mottled stems, deep, jaggedly serrate leaves, and well developed lateral branches. Since these characters are not limited to this region, and it is difficult to distinguish it from herbarium specimens there seems to be little to be gained by maintaining *H. annuus* subsp. *texanus*. Scheele's *H. lindheimerianus* is apparently the earliest name for this sunflower.

F. Plants frequently less than a meter tall, little branched, and characterized by more pubescence, particularly evident on the phyllaries which are often hirsute to villous, are found in the Rockies at altitudes of about 4500 to 8000 feet. These races grow poorly at Bloomington, flowering earlier than other samples at heights of around 25 cm. and frequently produce a single head. It is thus probable that they represent a distinct ecotype.

G. A fairly distinctive sunflower, originally described as a species, *H. jaegeri* (Heiser, 1948), and later reduced to a subspecies is perhaps worthy of continued recognition. It is distinguished by the very small heads (1.5-2.0 cm.), narrow phyllaries (3-4 mm.) which are nearly glabrous as are the stems, the small achenes (3.0-3.5 mm.), the few rays (10-15), and a tendency to have lanceolate or ovate-lanceolate leaves.

The distributional data given in the map are probably far from complete because the recognition of this "race" occurred late in this study and many specimens of this species may have been lumped with *H. annuus* ssp. *lenticularis*. Ecologically this sunflower is also rather distinctive since it occurs in rather arid regions but always near swampy areas or irrigation ditches. From the examination of populations in southern California and southern Utah it is clear that intergradation occurs with other types of *H. annuus*.

H. The sunflowers which occur throughout the remainder of the western United States extending into Canada and Mexico show a great deal of variability but no clear-cut "races" are discernible at present. Although the description does not completely agree with the figure given, it is fairly certain that the name *H. lenticularis* Dougl. belongs to this group. The type locality is given as interior and west coast of North America. In 1908 Cockerell proposed the combination *H. annuus lenticularis* and in 1954 I accepted this as a subspecies. In 1960 Boivin[3] reduced *H. lenticularis* to a form and in the same year Steyermark transferred it to varietal status. Neither author gave reference to the earlier nomenclatural transfer. However, whether "lenticularis" is treated as subspecies, variety, or form is of minor importance and does little to advance our knowledge of this sunflower.

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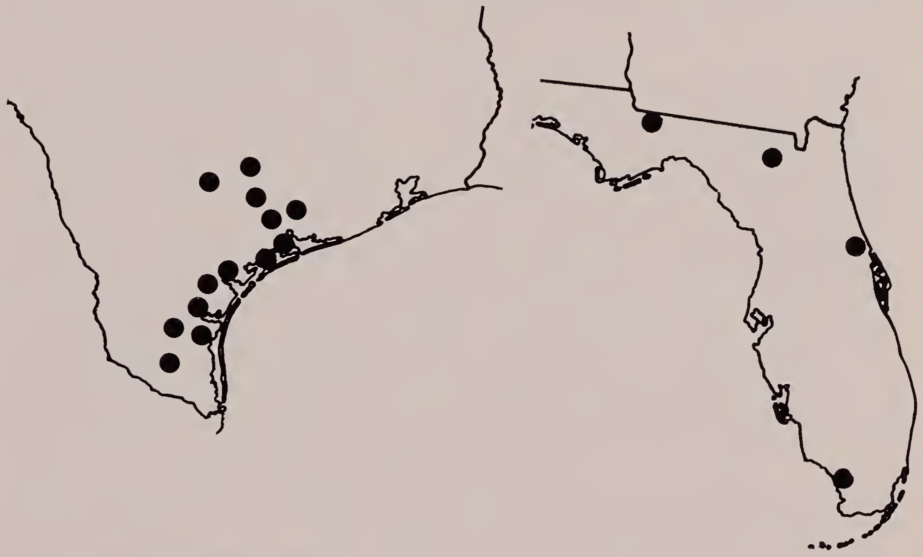
[3] In the same place Boivin describes a form, *fallax*, which differs from subspecies *lenticularis* "corollis aurantiacis." I assume that he is referring to the corollas of the disk flower. My crosses between forms of *H. annuus* with yellow disk-flowered corollas and purple disk-flowered corollas give approximate ratios of 1 purple, 2 red, and 1 yellow in the F_2 so it appears that a single gene controls this character. It is highly questionable to me that single gene differences

Natural hybrids of *Helianthus annuus* are known with *H. argophyllus, H. bolanderi, H. debilis, H. paradoxus, H. petiolaris, and H. praecox.* Artificial hybrids have been secured with all the above named annual species, *H. neglectus*, and with the perennials *H. decapetalus, H. hirsutus, H. strumosus,* and *H. tuberosus.*

8. Helianthus argophyllus Torrey and Gray, Fl. N. Am. 2:318. 1842. (Texas: *Drummond*, NY!)

H. annuus var. *argophyllus* Alef., *fide* Satsyperov, Bull. Appl. Bot. 9:207. 1916.



Map 8. *Helianthus argophyllus*

Annual; 1.0-3.0 m. tall; stem densely white tomentose to floccose, much branched; leaves ovate to ovate lanceolate, entire or shallowly serrate, truncate to subcordate, 15-25 cm. long, nearly as wide, densely pubescent with long silky hairs, petiolate; heads 2.0-3.0 cm. in diam.; phyllaries ovate

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are worthy of recognition. Moreover, if the yellow form deserves a name should not the red and purple forms also be designated, and then for consistency should not the two color forms in the cultivated sunflower also be recognized? Thus it is apparent that if one starts naming forms there is practically no end in sight. Fortunately, the number of taxonomists who continue to recognize forms by Latin names seems to be decreasing.

to ovate-lanceolate, abruptly long attenuate, densely white villous, tomentose or floccose, 5-7 mm. broad; rays yellow to orange-yellow, 15 or more; disk flowers usually deep purple; pales 3 cuspidate, middle cusp attenuate, glabrous or lightly villous; achenes obovate, somewhat flattened, 4-6 mm. long.

Chromosome number: n = 17

Distribution: in sandy soil, eastern Texas and adventive in Florida and perhaps elsewhere. Aug.-Oct.

This species is readily distinguished from all other sunflowers by the dense silvery white pubescence of the stems, leaves, and phyllaries. Except for the difference in pubescence, the nearly entire leaf and the flatter achene, it is very similar to some forms of *H. annuus*. *Helianthus niveus* also has a dense white pubescence composed of shorter hairs and it is likely that the pubescence of the two species represents a parallel development rather than origin from a recent common ancestor.

This species is sometimes cultivated as an ornamental for the striking effect of the foliage. It seems likely that the occurrence of this species in Florida as a weed today represents escapes from cultivation although this cannot be definitely proven. The earliest collection from Florida is in 1893 from "cultivated land."

I have also seen one collection from North Carolina (Brunswick Co., *Wilbur 6309*. DUKE), but I do not know if it is now established there. The Bodger Seed Co. informed me that they had been sent seeds of this from Australia by a collector who recommended it as a native Australian plant of possible ornamental value! Plants grown from seed they sent me were definitely *H. argophyllus*. The Florida sample (*Heiser 4039*) grown differs little from the Texas plants except in being shorter and having more coarse pubescence; crosses between plants from the two areas gave fully fertile hybrids. Sister crosses of the Florida race gave yellow disked segregates in later generations and certain of these have proven to be self-compatible whereas Texas races are self-incompatible.

Natural hybrids between *H. argophyllus* and *H. annuus* are known from Texas (Heiser, 1951a), and B. L. Turner (letter, 1959) has grown plants of *H. argoyphllus* which suggested past hybridization with *H. debilis* ssp. *cucumerifolius*. Artificial hybrids of *H. argophyllus* have been secured with both of the above named species and with *H. neglectus*, *H. niveus* and *H. petiolaris* as well as with the tetraploid perennial, *H. hirsutus*. The highest fertility of any of the hybrids was with *H. annuus*. This, along with the morphological similarity, indicates a very close relationship of the two species.

Attempts have been made to transfer the red ray color of *H. annuus* to *H. argophyllus* since it was thought the red color combined with the silvery leaf of *H. argophyllus* would make an attractive ornamental. After four

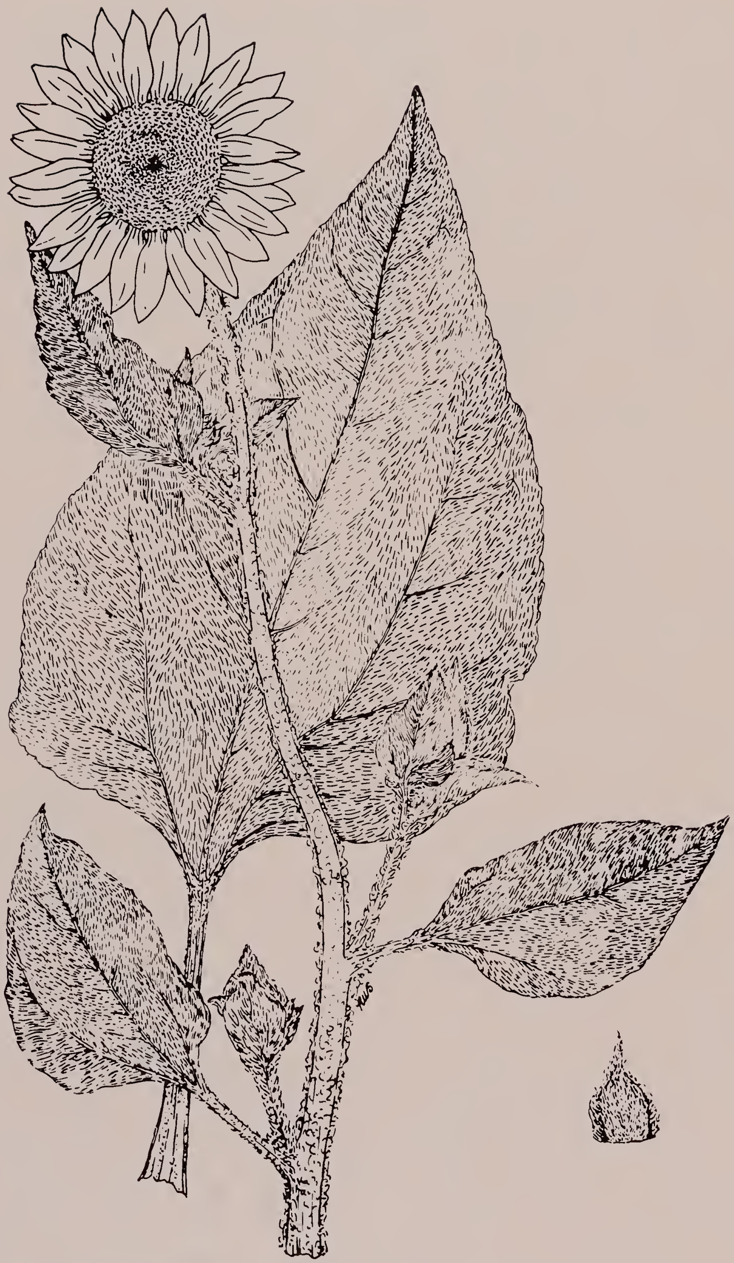
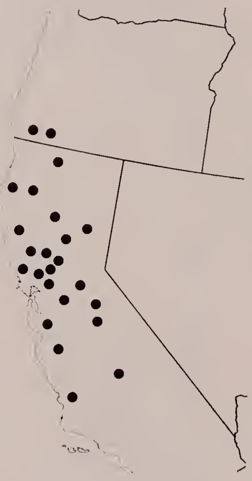


Fig. 8. *Helianthus argophyllus*

generations a plant was obtained with 50% fertility but it had only a very dilute red in the rays and the pubescence was far less pronounced than in *H. argophyllus.*

9. Helianthus bolanderi A. Gray, Proc. Amer. Acad. 6:544. 1865. (T.: Calif. Lake Co.; *Bolander 3958* GH!)

H. scaberrimus Benth. Bot. Voy. Sulphur, 28. 1844. (not Ell.)
H. exilis A. Gray, Proc. Amer. Acad. 6:545. 1865. (T.: Calif. Lake Co. *Bolander 2623* GH!)



Map 9. *Helianthus bolanderi*

Annual to 1.5 m. tall; stem hispid to hirsute; leaves linear-lanceolate to ovate, cuneate to truncate at base, entire to prominently serrate, hispid to sparingly hirsute on both surfaces, blade to 15 cm. long, 12 cm. wide, usually much smaller, petiolate; disk 1.5-2.5 cm. in diam.; phyllaries oblong to lanceolate, gradually attenuate, hirsute to hirsute-villous, generally conspicuously exceeding disk in length, 3.0-4.5 mm. broad; rays 10-17, usually bifid at apex; lobes of disk-corollas red-purple or yellow; pales 3-cuspidate, middle cusp subulate, conspicuously exceeding disk flowers, glabrous at tip; achenes 3.0-4.5 mm. long.

Chromosome number: n = 17

Distribution: generally in dry soil, low fields and foothills, southeastern Oregon to south central California. July-Sept.

A detailed treatment of this species has appeared elsewhere (Heiser, 1949) and little needs to be added here. This species shows considerable variation but far less than *H. petiolaris, H. debilis* and *H. annuus.* The hirsute phyllaries and the long, erect glabrous pales of the receptacle serve rather readily

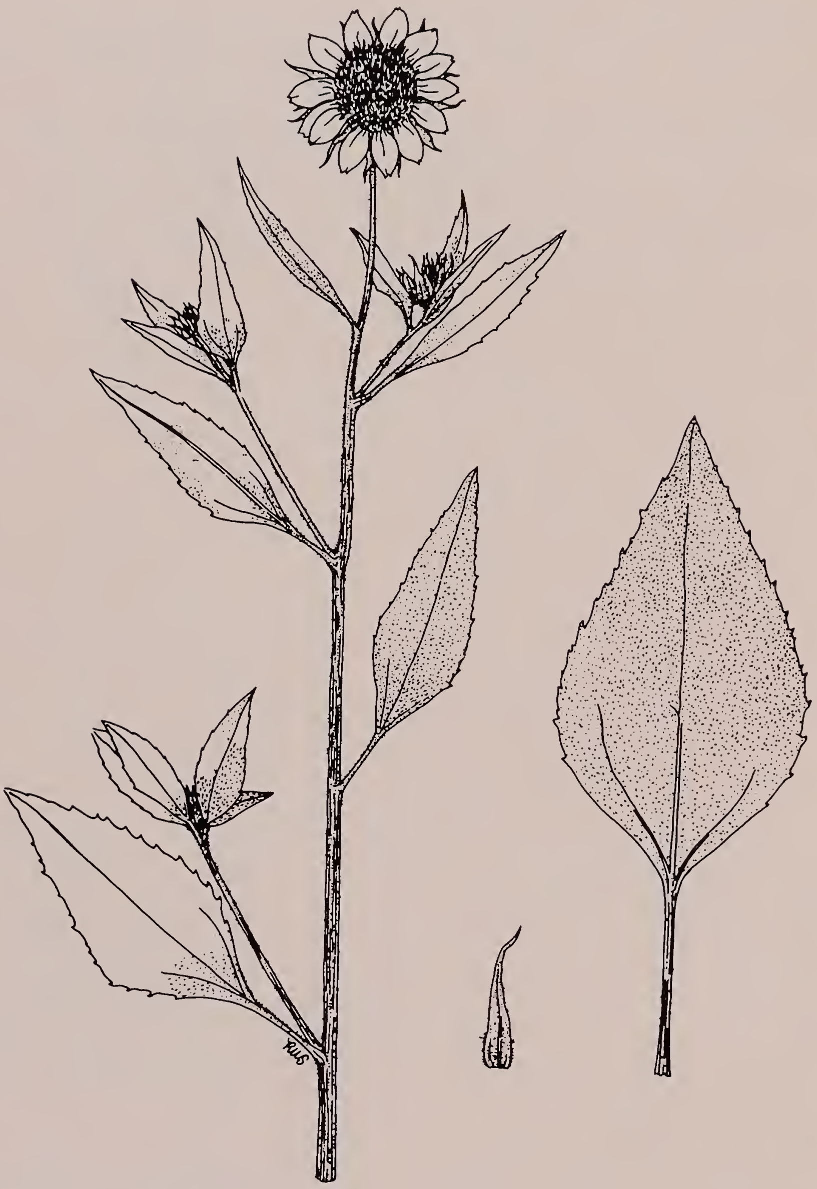
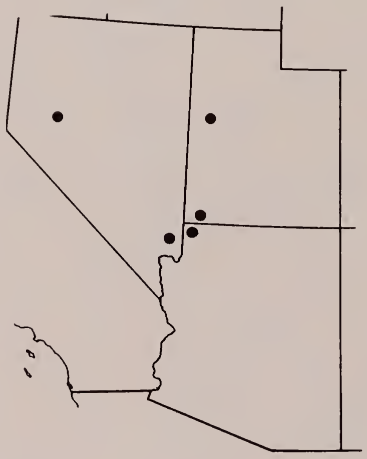


Fig. 9. *Helianthus bolanderi*

to distinguish it. It does not show particularly close relationship to any other annual species.

Natural hybridization with *H. annuus* is known, and it has been postulated that the weedy valley form of this species is a result of introgression from *H. annuus*. Certain hybrid populations near Davis, California have been subject to a detailed study by Stebbins and Daly (1961). This species is allopatric with all of the other annual species. Artificial hybrids have been secured with *H. annuus, H. debilis, H. praecox, H. niveus,* and *H. petiolaris.*

10. Helianthus deserticola Heiser, Proc. Ind. Acad. Sci. 70:209. 1960.[4]
(T.: Utah, Washington Co.; *Stoutamire 2574,* IND!)



Map 10. *Helianthus deserticola*

Annual; 0.1-0.4 m. tall, stem green or red, little branched, densely hispid; leaves lanceolate to lanceolate-ovate, cuneate at base, densely hispid-hirsute, entire, 2.5-5.0 cm. long, 1.0-2.0 cm. wide, petiolate; heads several, disk 1.3-2.5 cm. in diam.; phyllaries lanceolate to linear-lanceolate, short-acuminate, slightly exceeding disk, mostly 1.4 cm. long by 2 mm. wide; rays 9-12, 1.0-2.0 cm. long; pales hirsute at apex, rarely glabrous; achenes 4-5 mm. long, slender, pilose with hairs 0.5-1.0 mm. long; pappus of 2 awns, about 2.5 mm. long, and several ovate squamellae, 0.5-1.0 mm. long.

Chromosome number: n = 17

Distribution: Utah, Nevada to northwestern Arizona, 2100 to 4500 ft. May-Oct.

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[4] Erroneously as *H. deserticolus* in the original description. My attention was called to this mistake by both A. Cronquist and L. Shinners.

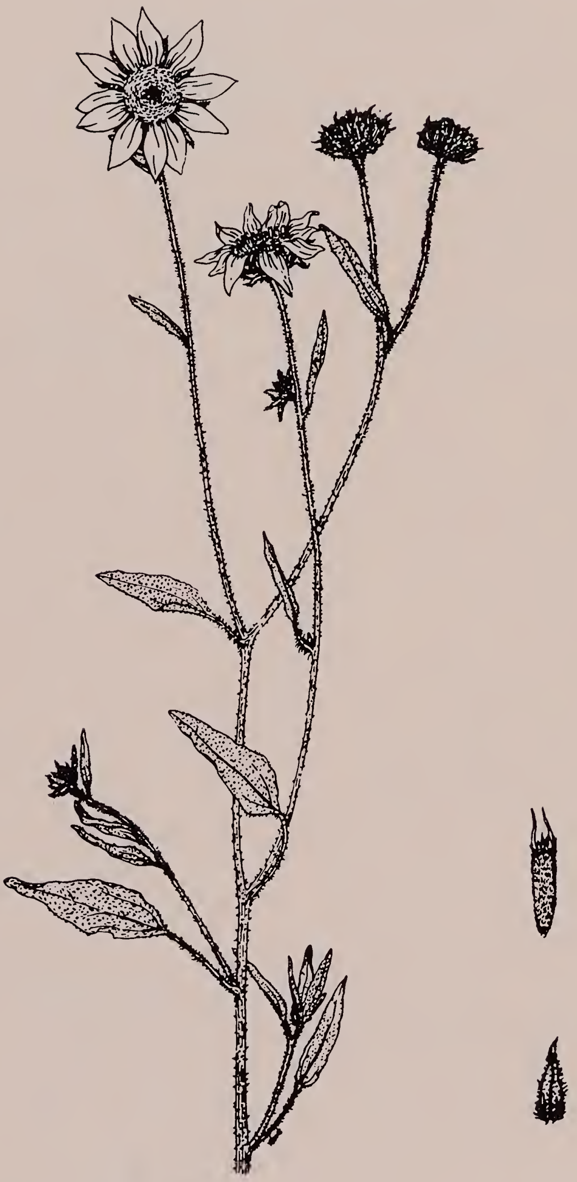
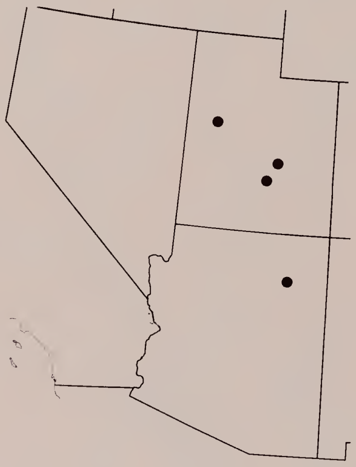


Fig. 10. *Helianthus deserticola*

This sunflower may be related to *H. anomalus* as was previously suggested (Heiser, 1960b) but it is probably equally close to *H. petiolaris*. The larger size of most characters and the pronounced tuberculate hairs of *H. anomalus* serve to separate that species quite readily from *H. deserticola*. Although the pales are usually pubescent in *H. deserticola*, they are not as densely so as in *H. petiolaris* and the pubescence of the stem and leaf of *H. petiolaris* is never as dense as that of *H. deserticola*. Depauperate specimens of *H. annuus* might be confused with this species, but the broader bracts of *H. annuus* which are generally somewhat ovate should serve as a means of distinguishing the two.

Seeds of *H. deserticola*, like those of the other xerophytic species of the genus, are difficult to germinate under artificial conditions. A few plants have been obtained and crosses attempted with three other annuals. Seed from the crosses failed to germinate.

11. Helianthus anomalus Blake, Wash. Acad. Sci. Jour. 21:333. 1931. (T.: Utah: Wayne Co., *Stanton 328*, US!)



Map 11. *Helianthus anomalus*

Annual, 2.5-6.0 dm. tall, stems whitish or greenish, somewhat glaucous, nearly glabrous or tuberculate-hispid, sparingly branched, leaf blades ovate or ovate-lanceolate, sparingly tuberculate-hispid, entire, cuneate at base, 5.0-10.0 cm. long, 3-6 cm. wide, petiolate; phyllaries linear-lanceolate, conspicuously long ciliate on lower margins, sparsely so on backs, 2.0-4.0 mm. wide, 1.5-2.5 cm. long, usually greatly exceeding the disk; heads few, disk 2.0-2.7 cm. in diam.; rays few, light yellow, 2.0-3.0 cm. long; pales long attenuate, hispid to near summit; achenes 6-9 mm. long, slender, buff-colored, densely villous with hairs 1-2 mm. long; pappus of several linear scales,

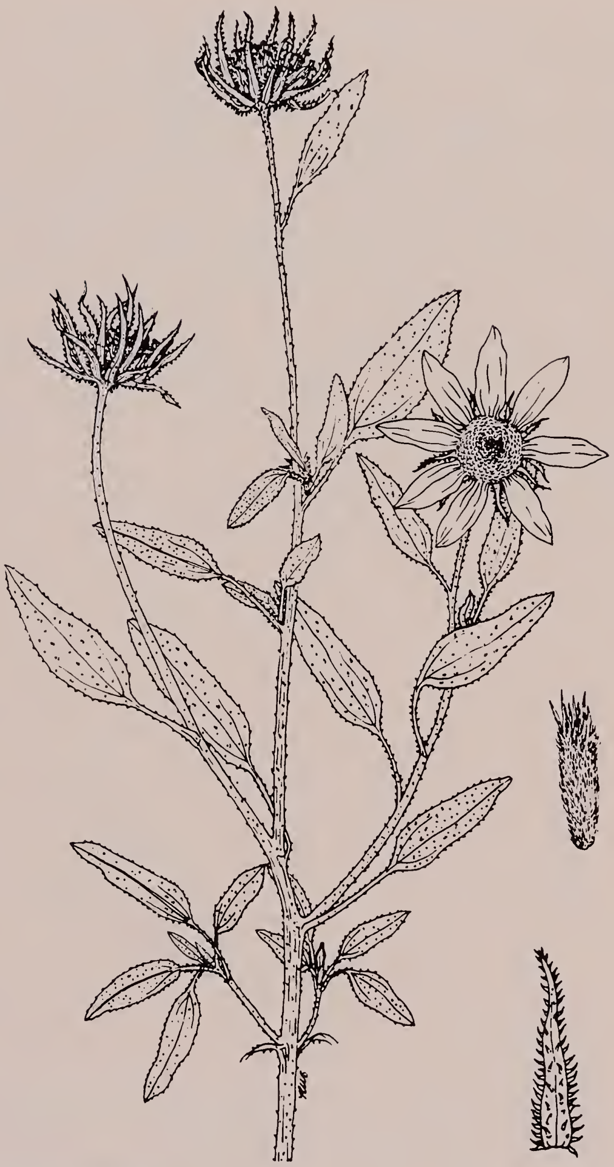


Fig. 11. *Helianthus anomalus*

generally two longer ones to 4.5 mm. and several shorter ones from 1-2 mm. long.

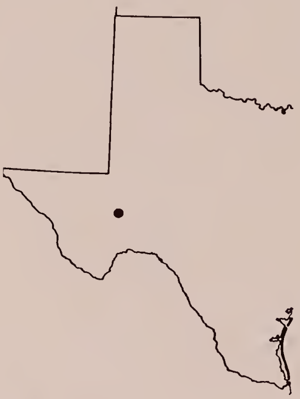
Chromosome number: n = 17

Distribution: Utah and northern Arizona, 4500-5000 ft. May-Oct.

Although a variety of techniques have been employed, great difficulty has been experienced in germinating seeds of the species. A few plants have been obtained and crosses have been attempted with *H. annuus*, *H. debilis*, *H. deserticola*, and *H. petiolaris* ssp. *fallax*. Some seed were obtained in all these crosses but only those involving *debilis* and *petiolaris* germinated. Five hybrids were secured with *H. debilis* ssp. *debilis* and they gave pollen stainabilities from 30 to 60% but no seed set in sister crosses. The one hybrid with *H. petiolaris* showed 2% pollen stainability. One specimen (Utah: Juab Co., *Harrison 351H*, MO) has been seen which might represent a natural hybrid with *H. deserticola*.

This is a most distinctive species and its closest relative is probably *H. deserticola* from which it may readily be distinguished by its larger size and the nature of the pubescence. Attention should be called to the similarity of the achenes of this species to those of *H. niveus* ssp. *tephrodes*.

12. Helianthus paradoxus Heiser, Rhodora 60:272. 1958. (T.: Texas, Pecos Co., *H. R. Reed*, Sept. 11, 1947, US!)



Map 12. *Helianthus paradoxus*

Annual 1.3-2.0 m. tall, stem nearly glabrous to hispid, branched above, branches rather short; leaves[5] lanceolate to ovate-lanceolate, cuneate at base, to 17.5 cm. long by 8.5 cm. wide, usually much smaller, scabrous, entire or lowermost remotely serrate or with a few prominent teeth, upper leaves

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[5] The original description erroneously gave the leaves as "opposite above, alternate below" whereas exactly the opposite is true.

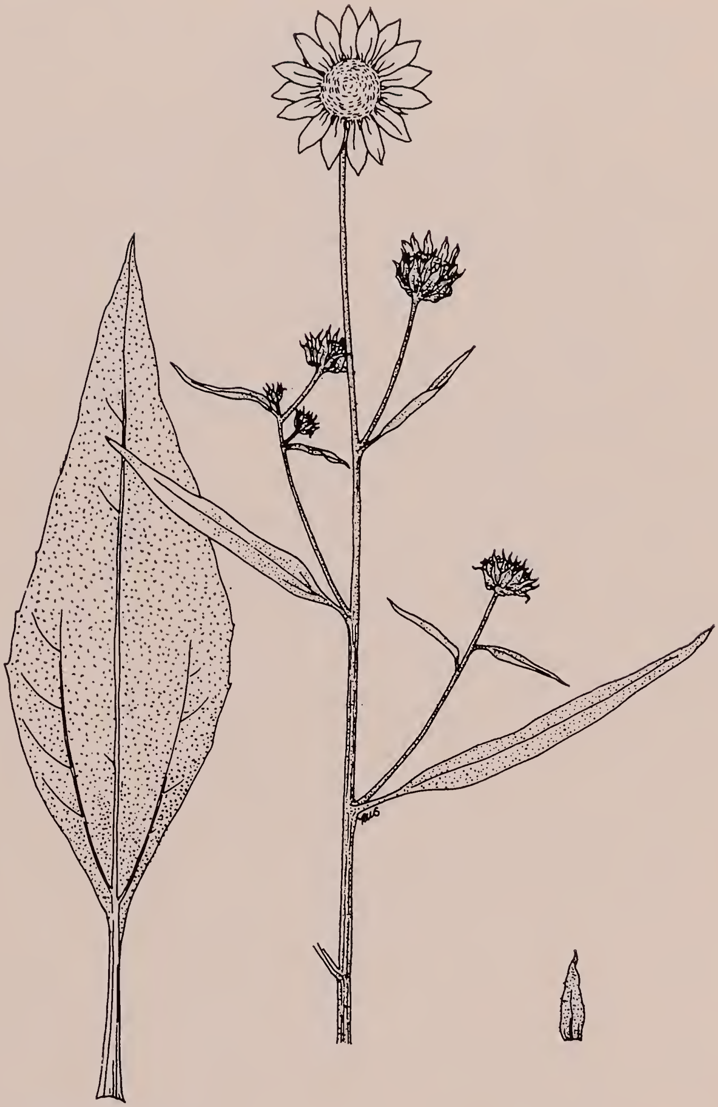


Fig. 12. *Helianthus paradoxus*

much reduced, those of the inflorescence bract-like, petiolate; phyllaries 15-25, spreading or slightly recurved at tips, oblong-lanceolate, acuminate, sparingly scabrous or hispid, margin ciliate with gland tipped hairs or hispid, about equalling disk, 3-4 mm. wide; disk 1.4-2.0 cm. in diam.; rays 12-20; pales glabrous at tips; achenes 3-4 mm. long, glabrous.

Chromosome number: n = 17

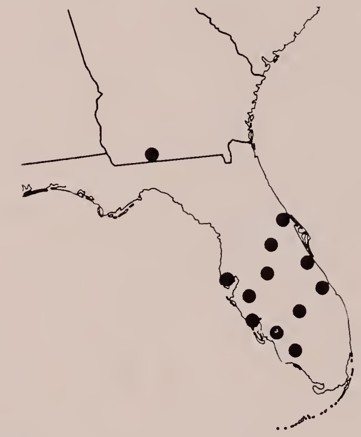
Distribution: Pecos Co., Texas. Sept.-Nov.

Although coming from a fairly arid region, this sunflower grows only in wet places, and greenhouse observations indicate that an abundance of water is necessary for good growth. With the original description it was pointed out that this species appears to be most nearly related to *H. petiolaris* and *H. annuus* but this relationship does not appear to be a close one. This species suggests *H. agrestis* in general growth habit and the glabrous or nearly glabrous condition of certain parts. The resemblance here, however, could represent a parallel development in adaption to wet soils rather than a close phylogenetic connection. Natural hybrids are known with *H. annuus* which show very low fertility. From both *H. annuus* and *H. petiolaris* this species is distinguished by its glabrous pales, leaf and phyllary shape, and the late flowering.

Artificial hybrids with pollen fertilities ranging from 4 to 25% have been secured with *H. annuus*, *H. argophyllus*, *H. debilis*, and *H. praecox*.

In addition to the specimens cited with the original description and later (Heiser, 1965a) one other specimen, *Bigelow 570* from Escondido Creek (NY) has been seen which is referable to this species.

13. Helianthus agrestis Pollard, Proc. Wash. Biol. Soc., 13:184. 1900. (T.: Volusia Co., Fla.; *Curtiss 6741*, US!)



Map 13. *Helianthus agrestis*

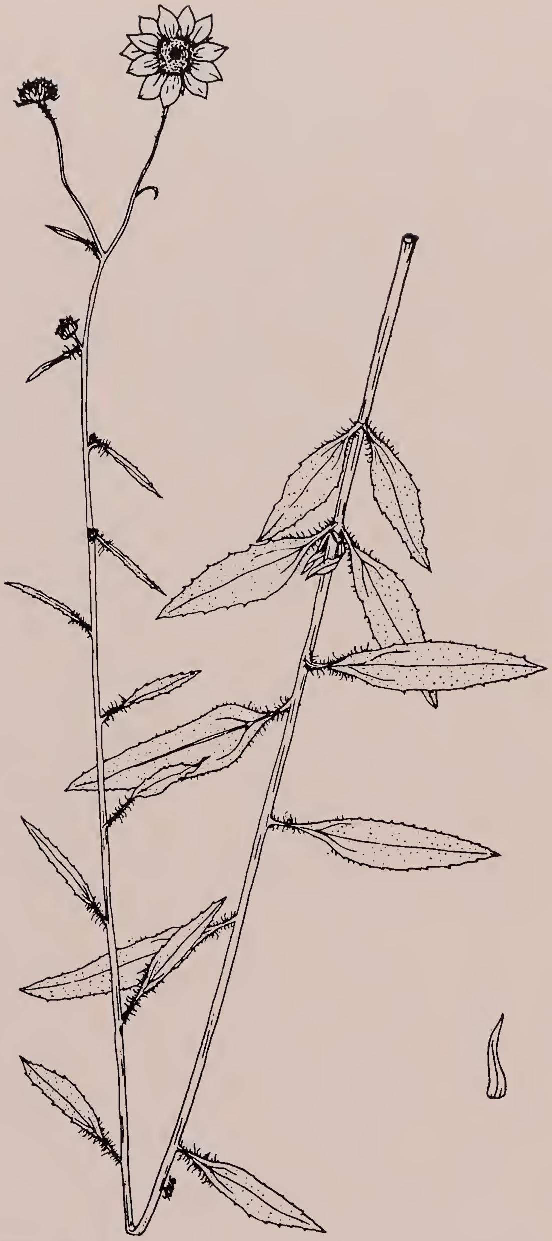


Fig. 13. *Helianthus agrestis*

Annual from shallow root system, 1 rarely 2 m. in height, branches slender; stem and branches glaucous and glabrous or with a few scattered hairs; leaves lanceolate, acuminate, mostly opposite, becoming alternate near heads, 8.5-18.0 cm. in length, 1.5-4.0 cm. in width, thin, light green both sides, shiny, irregularly and usually sparingly serrate, teeth mucronate, petiole quite short, 5-12 mm. in length, prominent scattered long, stiff white hairs principally along lower margin and petiole; peduncles slender, short tomentose near summit; disk conical, about 1.0 cm. in diam. or slightly larger; phyllaries lanceolate, acuminate, usually somewhat longer than the disk, loose but not reflexed, hispidulose along the margins, otherwise glabrous, 1-2 mm. broad, rays 12-18 mm. in length; lobes and throat of disk florets purple; style branches yellow; anthers purple; pales glabrous; achene 2-3 mm. long, glabrous and inconspicuously tuberculate.

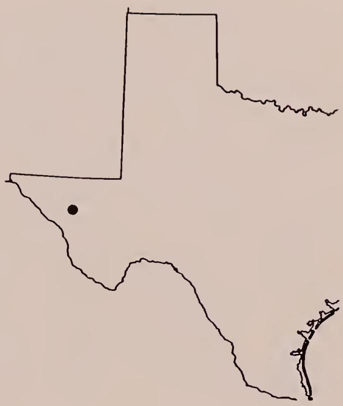
Chromosome number: n = 17

Distribution: in mucky, wet soil, Thomas Co., Georgia and central Florida; July-Dec.

This is a remarkably uniform species and it does not appear to be at all closely related to the other annuals, with the possible exception of *H. paradoxus*. Numerous attempts at hybridizing the species with all other annuals have failed. The only artificial hybrids obtained involving this species were with *H. simulans* (reported as *H. angustifolius* in Heiser, 1965a). All fourteen hybrids showed abnormal development and failed to produce any pollen but survived as perennials for several years. It could be that this species is derived from the perennials rather than being directly related to the other annuals. In fact, it might be questioned whether or not it is a *Helianthus*. The receptacle is definitely more conical than in other species of *Helianthus*, the somewhat tuberculate achene is unique for the genus and the chromosomes are slightly larger than those of other species. This species is also unusual in that it is the only species known to be highly self-compatible. Few seed are set in the greenhouse, however, unless the heads are rubbed so it is probable that insect visitors are required for natural pollination. The plant requires high humidity for its best growth and wilts promptly when collected in the field. Although a few plants have been collected in nature in flower in late July, these seem to be exceptional. The two strains grown at Bloomington have never flowered before October.

Chapman's concept of *H. floridanus* (Fl. South, U.S., Suppl. 629. 1884) included material of this species (Fla., *Chapman*, GH).

14. Helianthus ludens Shinners, Sida 1:377. 1964. (T.: Texas, Culberson Co., *Turner, Tharp* and *Warnock 53-543*, SMU!)



Map 14. *Helianthus ludens*

Stems to 43 cm. tall, hispid-hirsute above with slender appressed hairs and scattered straight thicker hairs to 1 mm. long, branching mostly above; leaves alternate, blades lanceolate, sinuate-dentate to subentire, 3 nerved, strigose, to 8 cm. long by 1 cm. wide, petioles to 1.8 cm. long, ciliate; heads few on peduncles to 12 cm. long; disk 1.0 to 1.2 cm. in diam.; rays apparently few (10-12?), ca. 1.2 cm. by 4 mm., drying light yellow; phyllaries linear-lanceolate, short attenuate, outer loose but not reflexed, equalling or very slightly exceeding disk, dark and light green striate, hispid-hirsute, to 10 mm. long by 2 mm. wide; disk-flowers yellow, glabrous above, pubescent in lower third; stigmas yellow; anthers dark; pales 3-cuspidate, glabrous or with a few scattered short hairs, middle cusp long attenuate, nearly equalling disk-flowers; achenes dark mottled, to 3 mm. long, sparingly strigose; pappus of 2 to several short lacerate scales, to 0.5 mm. long.

Chromosome number: not known

Distribution: Texas, Culberson Co., Lobo Flat, 19 miles east of van Horn. Known only from type collection. August.

As the author of this species points out it has the aspect of a *Viguiera* or *Verbesina*. It is certainly very unlike any other species of *Helianthus*. Dr. Marshall T. Johnston of the University of Texas informs me (in litt.) that he is transferring it to the genus *Viguiera*, and I must agree that this is probably a better place for it than *Helianthus*.

In addition to the type specimen there are two duplicates at the University of Texas. The achenes on the type are immature but both isotypes bear mature achenes. In one of these (Texas #155582) the pappus is somewhat persistent, which would support the placement in *Viguiera*; but on the second sheet (Texas #179473) the pappus is readily deciduous, which would place it in *Helianthus*. Except for very slight differences in density of pubescence,

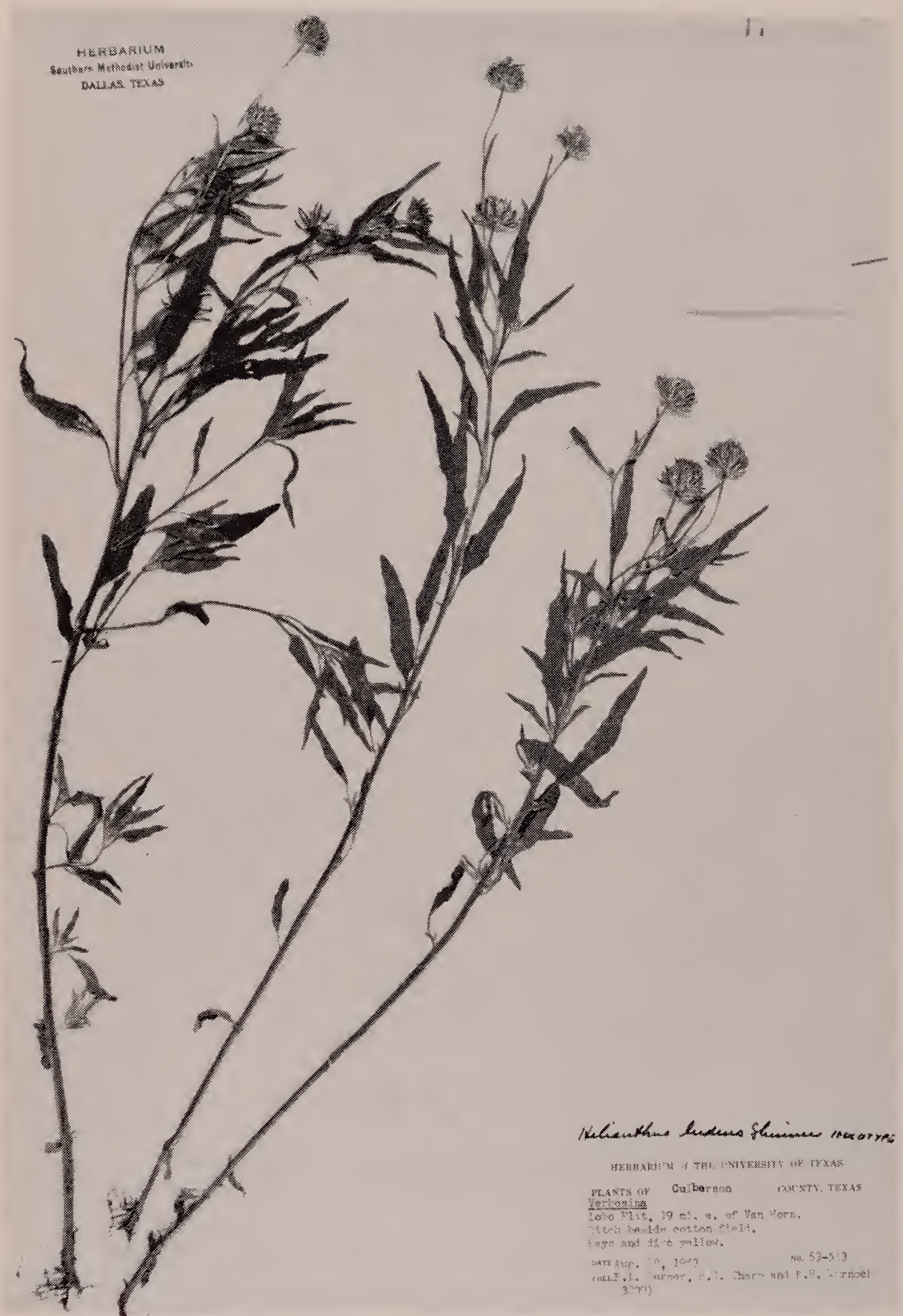

HERBARIUM
Southern Methodist University
DALLAS, TEXAS
Helianthus ludens Shinners
HERBARIUM OF THE UNIVERSITY OF TEXAS
PLANTS OF Culberson COUNTY, TEXAS
Lobo Flat, 39 mi. e. of Van Horn.
Ditch beside cotton field.
Rays and disc yellow.
DATE Aug.
NO.

Fig. 14. *Helianthus ludens*

the specimens otherwise appear identical. The fact that all the pappus scales are nearly equal instead of two of them being definitely longer is rare in both *Helianthus* and *Viguiera*.

In view of the close relationship of *Helianthus* and *Viguiera*, if indeed they should be considered separate genera, species such as this should come as no surprise, although they may be disturbing to those who desire clear cut generic lines. It is to be recalled that *H. similis* is another species that appears to be transitional between the two genera.

The species is treated here rather than being excluded in the hope that attention will be called to the need for additional study. Cytogenetic studies could help establish whether its nearest affinities are to *Helianthus* or *Viguiera*.

Since the plant was recorded as a weed in a cotton field, the possibility exists, of course, that it could represent a recent introduction into Texas. If it does prove to be an exotic, one might suspect Mexico as the source of origin.

Section II. Ciliares

Western North American perennials from tap roots or horizontal roots; rhizomes lacking; leaves mostly or all opposite.

Key to Series of Ciliares

Roots stout, leaves usually with evident petioles, mostly Rocky Mts. and western United States..1. Pumili

Roots slender, horizontal roots present giving rise to new plants; leaves usually sessile or subsessile, southwestern United States and Mexico............................2. Ciliares

Series Pumili

Perennials with new growth from buds at base of old stem; leaves usually somewhat harshly pubescent.

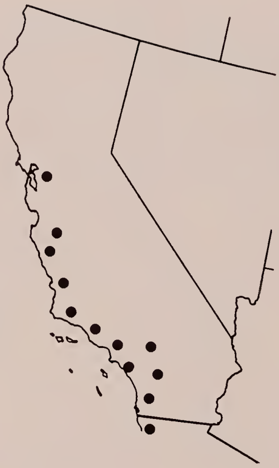
Key to Species of Pumili

Root thickened at apex, fleshy; phyllaries attenuate, exceeding disk in length; northwestern United States..17. *H. cusickii*

Root not unusually thickened and fleshy; phyllaries blunt to short-attenuate, about equalling disk or shorter

- Phyllaries glabrous or hispidulous; stems sparingly short-strigose-hispid or glabrous, usually red or purple; west central California to northern Baja California..15. *H. gracilentus*
- Phyllaries usually white strigose-hispid; stems usually long strigose-hispid, usually green; Rocky Mts...16. *H. pumilus*

15. Helianthus gracilentus A. Gray, Proc. Am. Acad. 11:77. 1876. (T.: Calif., San Diego Co., *Palmer*, GH!)



Map 15. *Helianthus gracilentus*

Stems 1-rarely 2 m. tall, sparingly strigose-hispid or rarely nearly glabrous; leaves all opposite, or uppermost alternate, lanceolate to lance-ovate, usually 1 or 3 nerved, hispid on both surfaces, entire, serrulate or with few prominent teeth in lower half, 5-11 (-15) cm. long, 2.0-3.5 cm. wide, subsessile or with petioles to 3 cm; heads few on long slender peduncles; disk 1.3-2.0 cm. in diam.; phyllaries lanceolate to lance-ovate, appressed and somewhat graduate, equal to or shorter than disk, hispidulous to subglabrous on backs, ciliolate on margins, 1.5-2.5 mm. broad; lobes of disk-corolla yellow or red; pales entire or shallowly 3-cuspidate, middle cusp short acute, ciliolate at tip; achene 3-4 mm. long.

Chromosome number: $n = 17$

Distribution: dry slopes, near the coast from Contra Costa Co., Calif. to northern Baja Calif., near sea-level to 4700 feet. May-Oct.

This is a well marked species, well set off, both morphologically and geographically, from its nearest relative, which is probably *H. pumilus.* Artificial hybrids obtained between the two species however, show rather greatly reduced fertility. The artificial hybrids secured with *H. laciniatus* give slightly higher pollen stainabilities.

No detailed field studies of this species have been made but the herbarium specimens examined indicate considerable variability in the species. It is unlikely that hybridization, unless it be very ancient, is responsible for the variability, since there are few other species of *Helianthus* found in its present range and it is unlikely that natural hybrids occur with any of these.

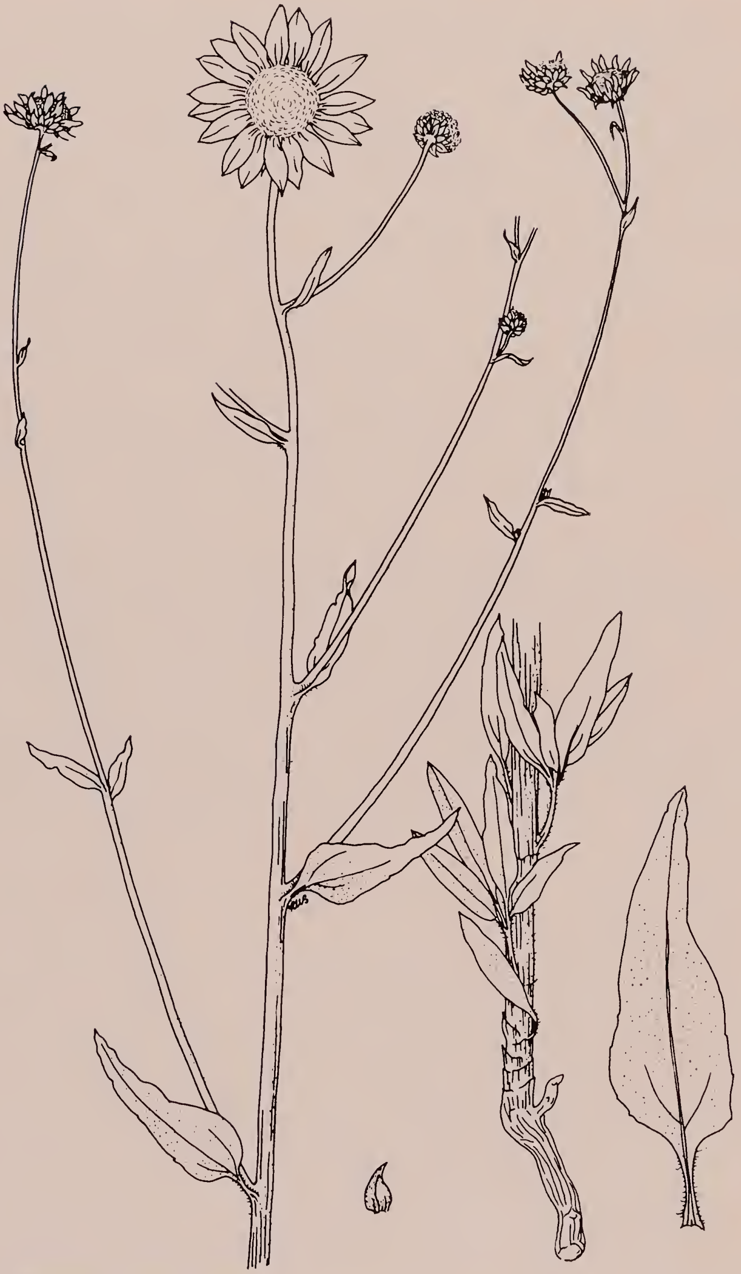
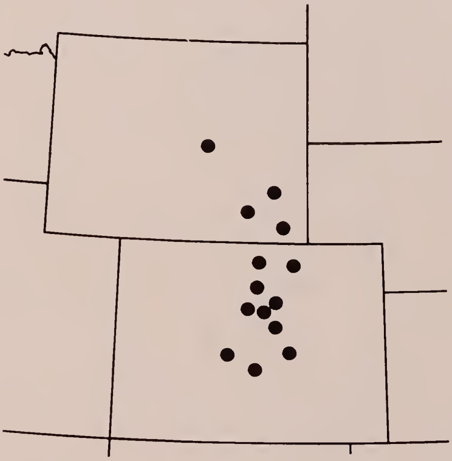


Fig. 15. *Helianthus gracilentus*

16. Helianthus pumilus Nutt. Trans. Am. Phil. Soc. n.s. 7:366. 1841. (T.: *Nuttall*, BM, photo, GH, IND!) (Not *H. pumilus* Pers. Syn. Pl. 2:475. 1807. publ. as syn. of *H. indicus*)

H. excubitor E. E. Wats. Pap. Mich. Acad. 9:396. 1929. (T.: Colorado: Clear Creek Co., *M. E. Jones 530*, F!)



Map 16. *Helianthus pumilus*

Stems 0.3-1.0 m. tall, scabrous-hispid to strigose, usually green, simple or branched above; leaves opposite, ovate to lanceolate, cuneate to rarely truncate, acute, usually 3-nerved, entire to serrate, coarse in texture, ashy green, strigose-hispid, 4.0 to 15.0 cm. long, 1.0 to 4.0 cm. wide, distinctly petiolate, petiole variable in length; heads few on rather short peduncles; disks 1.0-1.4 cm. in diam.; phyllaries lanceolate to ovate-lanceolate, acute to short acuminate, shorter than or equaling disk in length, sparingly to densely hispid or white strigose on backs and margins; rays few, light yellow; disk-corollas yellow; pales entire or shallowly 3-cuspidate, acute to acuminate, hispid at tip; achene 3-4 mm. long.

Chromosome number: n = 17

Distribution: dry, frequently rocky soil, central and southeastern Wyoming to central Colorado, 4000-6000 feet. July-Sept.

From *H. gracilentus* which appears to be its closest relative, *H. pumilus* is distinguished by its usually broader, more grayish green leaves, larger and fewer phyllaries, in addition to the differences noted in the key. No detailed studies of the variation of this species have been made but two intergrading groups can be distinguished in herbarium material, one having small heads

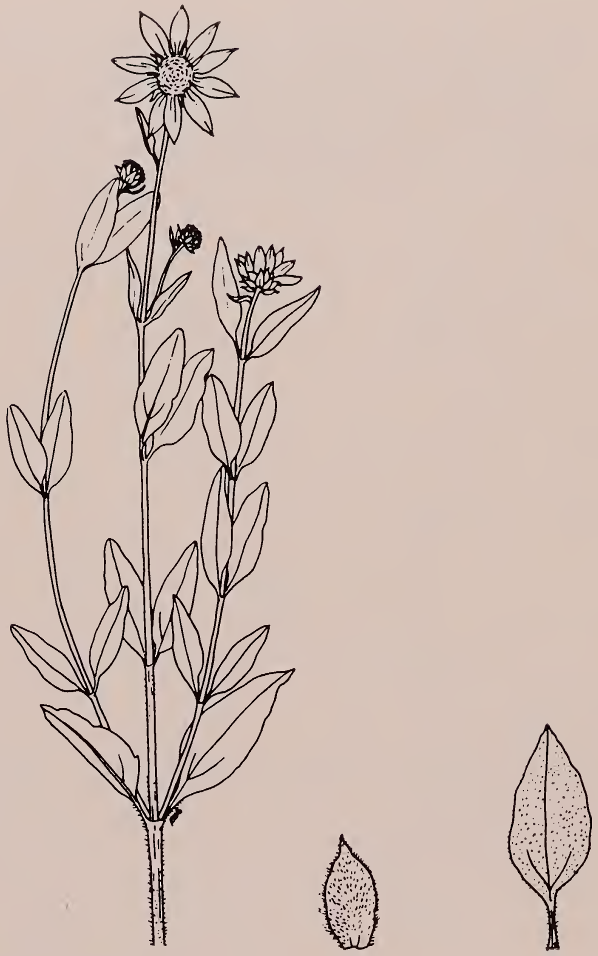


Fig. 16. *Helianthus pumilus*

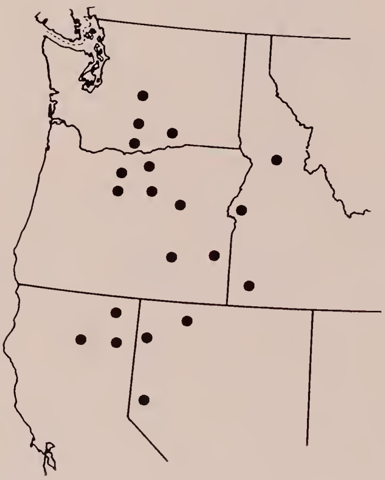
and narrow conspicuously graduated phyllaries, and the other with larger heads and broader, less clearly graduated phyllaries.

Artificial crossings have resulted in hybrids with *H. cusickii*, *H. gracilentus*, and *H. niveus*, all of which show considerable to great reduction in fertility. No hybrids have been secured in attempts at crossing with *H. nuttallii*, the only diploid perennial which is sympatric with *H. pumilus*. It therefore seems unlikely that natural hybridization occurs between the two, but the plant described by Watson as *H. excubitor* has some features suggesting that it might be derived from such hybridization. However, it is more likely that it is simply a somewhat atypical specimen of *H. pumilus*.

Two specimens are mounted on the type sheet of *H. pumilus*, the uppermost of which must be regarded as the holotype; the identity of the lowermost cannot be made out with certainty from the photograph but appears to be a somewhat depauperate specimen of *H. petiolaris*.

The type of *H. pumilus* var. ? *Nicolleti* T. & G. (Fl. N. Am. 2:331. 1841), a collection by Nicollet from near Devil's Lake in the Northwest Territory (North Dakota?), has not been located, but is probably at New York or Harvard. A specimen annotated as such (by Gray?), *Geyer 468*, "Nicollet's NW expedition, moist fertile prairies about Desoto" appears to be *H. maximiliani*.

17. Helianthus cusickii A. Gray, Proc. Amer. Acad. 21:413. 1886. (T.: Oregon, Malheur Co., *Cusick 1226*, GH!)



Map 17. *Helianthus cusickii*

Stems to 1.2 m. tall, erect or somewhat prostrate, glabrous or with long scattered hairs; leaves mostly or all opposite, linear-lanceolate to lanceolate,

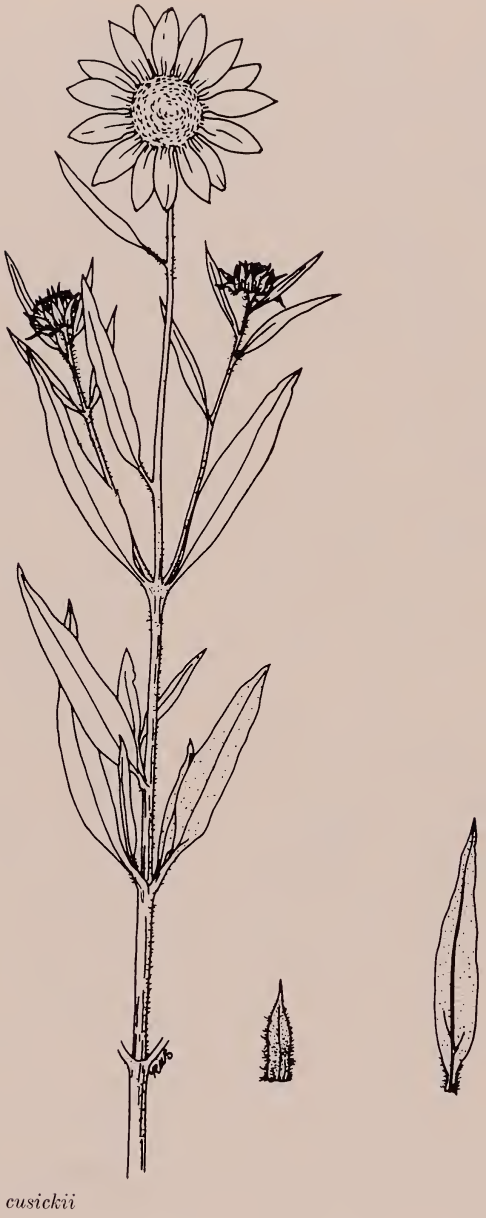


Fig. 17. *Helianthus cusickii*

frequently strongly 3-nerved, entire, scabrous-hispid to glabrous, blade 6.0-15.0 cm. long, 1.0 to 2.5 cm. wide, sessile or with very short petiole; peduncles one to few-flowered; disks 1.2-2.8 cm. in diam.; phyllaries usually few (12-18), lanceolate to oblong-lanceolate, generally exceeding disk in length, 3-4 mm. broad, appressed pubescent to densely hirsute; rays to 3.5 cm. long; lobes of disk corolla yellow; pales entire or shallowly 3-cuspidate, middle cusp acute, rarely acuminate, lightly pubescent; achene 4-5 mm. long.

Chromosome number: n = 17

Distribution: dry slopes and open woods, central Washington, eastern Idaho, south to northern Nevada and California. 2000-6500 feet. April-Aug.

This is a very distinct species whose most unique feature is the somewhat parsnip-like root. Superficially it appears rather similar to some of the northwestern species of *Helianthella*, and in certain characters of the head and pubescence it suggests *H. bolanderi*. However, in all probability it is most nearly related to *H. pumilus* and *H. gracilentus* which share with it the perennial habit, lack of rhizomes, and opposite, lanceolate leaves. This is also suggested by the results of limited hybridization tests. Pollinations with *H. bolanderi*, *H. divaricatus* and *H. nuttallii* failed to give seeds but three hybrids were secured with *H. pumilus* as the male parent. The hybrids averaged 30% pollen stainability and showed 17 pairs of chromosomes at diakinesis.

Series 2. Ciliares

Perennials from long-creeping roots; leaves frequently bluish or grayish green, sessile to short petiolate. (Although most authors have considered that a "rootstock" or rhizome is characteristic of these species, the structure giving rise to new plants is actually a root. Thus the union of these species with the Pumili, originally based solely on crossing behavior, is given additional support.)

Key to Species of Series Ciliares

Leaves and stems glaucous, usually glabrous, rarely somewhat hispid.

- Disk-corollas yellow; phyllaries mostly less than 3 mm. broad; plants generally 0.3 m. or less tall . . . . 18. *H. arizonensis*
- Disk-corollas usually red or red tipped; phyllaries mostly over 3 mm. broad; plants generally over 0.3 m. tall . . . . 20. *H. ciliaris*

Leaves glabrous or nearly so to strigose; stems rarely somewhat glaucous, usually hispid or strigose . . . . 19. *H. laciniatus*

18. Helianthus arizonensis R. Jackson, Brittonia 15:266. 1963. (T.: Arizona: Navajo Co., *Jackson 2674-1*, IND!)

Stems 0.2-0.3 m. tall, glaucous, green; leaves lanceolate, acute, undulate, glabrous and glaucous, bluish-green, 6-7 cm. long by 1.0-1.3 cm. wide; heads

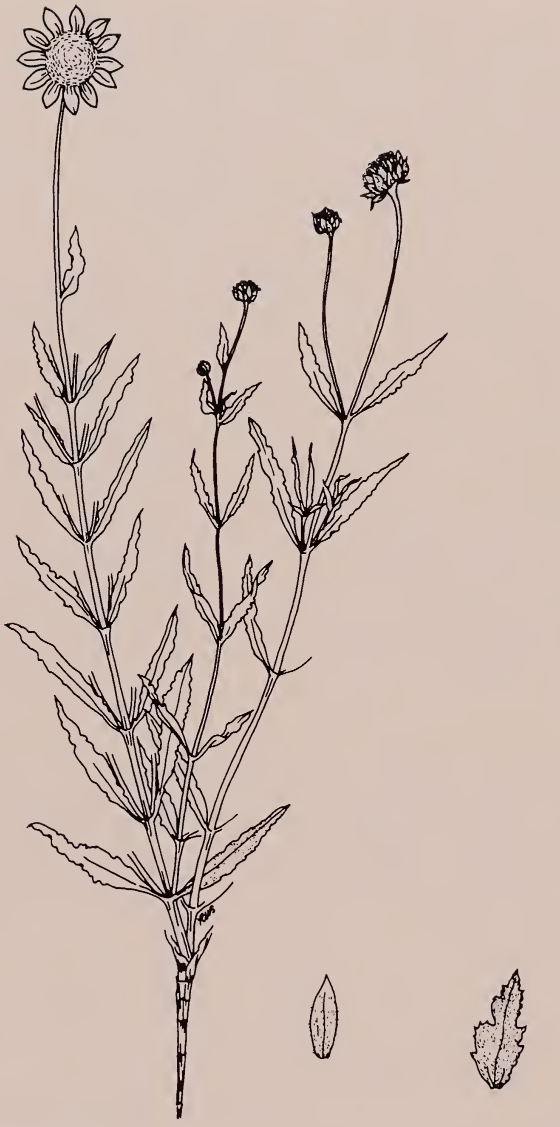
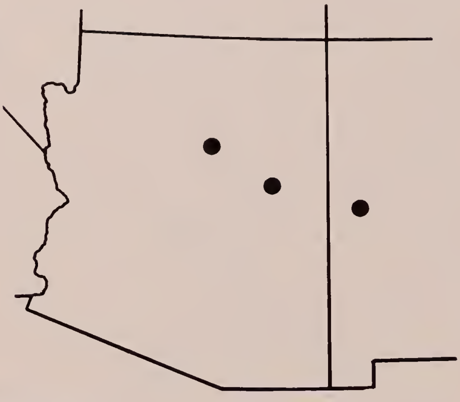


Fig. 18. *Helianthus arizonensis*



Map 18. *Helianthus arizonensis*

one to few; disk 1.0-1.8 cm. in diam.; phyllaries lanceolate, not strongly graduated, ciliate on margins and glabrous to puberulent on backs, nearly equalling disk in length, 2.0-2.7 mm. broad; rays few, small; disk corollas yellow; pales acute, entire, hispidulous; pappus of 2 ovate scales; achene ca. 3 mm. long.

Chromosome number: $n = 17$

Distribution: dry, frequently sandy soil, west central New Mexico to east central Arizona, 4000 to 7000 feet. June-Aug.

See discussion under *H. laciniatus* and *H. ciliaris*.

19. Helianthus laciniatus A. Gray, Mem. Am. Acad., n.s., 4:84. 1849. (T.: Mexico, Coahulia, Valley of Mazar, Bolsón de Mapiné, *Gregg 29*, GH!)

H. heiseri R. Jackson, Madroño 15:54. 1959. (T.: New Mexico. Grant Co., *Jackson 2521-1*, IND!)

H. laciniatus ssp. *heiseri* R. Jackson, Brittonia 15:268. 1963.

H. crenatus R. Jackson, Madroño 15:55. 1959. (T.: New Mexico. Sierra Co., *Jackson 2504-1* IND!)

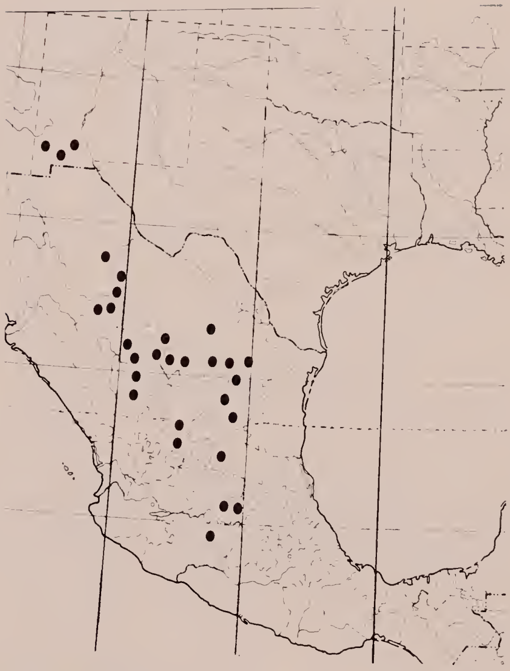
H. laciniatus subsp. *crenatus* R. Jackson, Brittonia 15:267. 1963.

H. dissectifolius R. Jackson, l.c. p. 268 (T.: Mexico, Durango. 3 mi. S. of Zarca, *Jackson 2916-2* IND!)

H. dissectifolius subsp. *longilobus* R. Jackson, l.c. p. 271. (T.: Mexico, Chihuahua, Camargo, *White 2772* GH)

H. dissectifolius ssp. *trifurcatus* R. Jackson, l.c. (T.: Mexico, Chihuahua, ca. 20 mi. N. of Camargo, *Jackson 2492-4* IND!)

H. dissectifolius ssp. *brevilobus* R. Jackson, l.c. (T.: Mexico, Chihuahua, ca. 50 mi. N. of Chihuahua, *Jackson 2496-1* IND!)



Map 19. *Helianthus laciniatus*

Stems 0.5-1.2 m. tall, subglabrous to strigose or hispid, usually light green, rarely somewhat glaucous above; leaves mostly opposite, but sometimes nearly all alternate, narrowly lanceolate and 1-nerved to broadly lanceolate and 3-nerved, acute, entire, serrate, or shallowly to deeply 3 to many lobed, sparingly to densely hispid, strigose or strumose, frequently resin dotted, often ciliate on margins, ashy green to light green, 5-9 cm. long, 0.5-3.5 cm. wide, cuneate at base; heads one to few; disks (0.8-) 1.2-2.4 cm. in diam.; phyllaries lanceolate to oblong, scarcely or slightly graduated, loosely appressed, ciliate, subglabrous to hispidulous or strigose on backs, about equalling disk in length, 2.5-3.3 mm. wide; rays 14-20, 10-12 mm. long; lobes of the disk corollas red or yellow; pales entire or shallowly 3-cuspidate, obtuse or acute, subglabrous to densely hispid-ciliate at tips; pappus of 2-5 linear or lanceolate scales; achenes 2.7-3.5 mm. long.

Chromosome number: n = 17

Distribution: Moderately dry to wet, frequently alkaline areas, Nuevo León, Mexico and southwestern New Mexico south to Michoacan, Mexico. June-Sept.

Although Gray described *H. laciniatus* he failed to include it in his Synoptical Flora and Watson (1929) treated it as a synonym of *H. ciliaris*. It is,

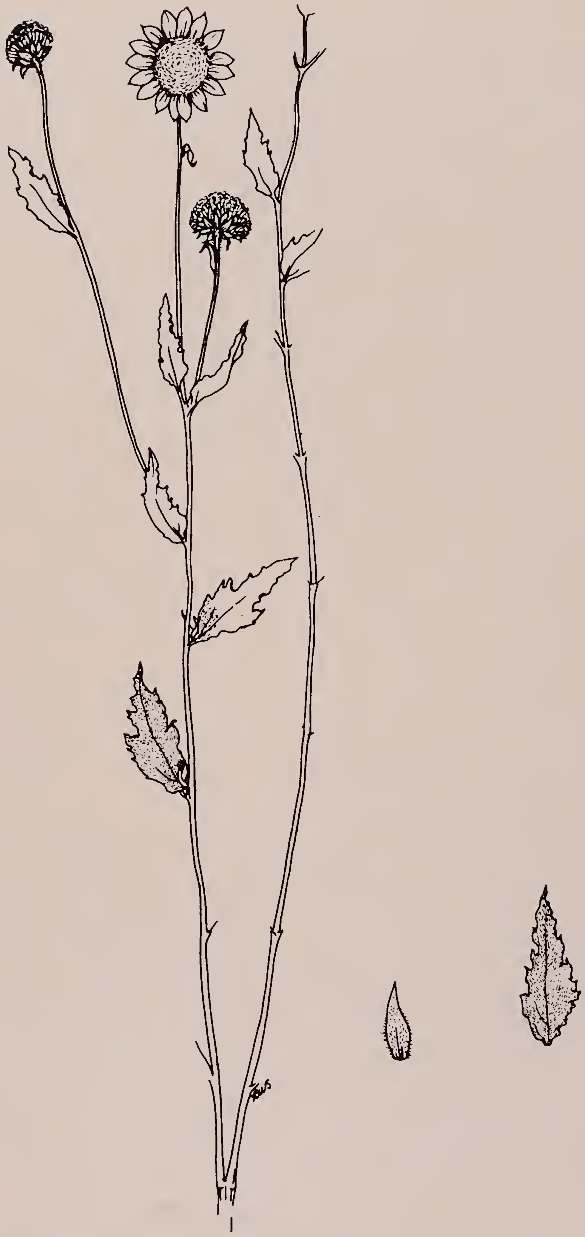


Fig. 19. *Helianthus laciniatus*

however, a very good and distinct species with its nearest relatives in *H. arizonicus* and *H. ciliaris.* It may have contributed one genome to *H. ciliaris.* Jackson (1963) has given monographic treatment to these species and has recognized several additional taxa, all of which I refer to synonymy under *H. laciniatus* which makes *H. laciniatus* an extremely variable species, but variable species, of course, are not unusual in this genus. Jackson's *H. dissectifolius* is distinguished from *H. laciniatus* on the basis of the leaf dissection and partly on glaucous or nonglaucous upper parts of the stems. Both of these characters are extremely variable and from an examination of a large number of specimens I would conclude that the variation is continuous so that it is impossible to demarcate two species. Under each of these species Jackson recognizes several subspecies. In his introduction (p. 262) he points out that "In *H. laciniatus*. . .it appears that separate valleys and distinct geographical areas may be occupied by minor morphological types. . ." It seems to me that his subspecies are hardly more than minor "morphological types," hence, not deserving of taxonomic recognition in keeping with the spirit of the taxonomic treatment of other species.

H. laciniatus has produced vigorous artificial hybrids in crosses with *H. arizonicus* and *H. gracilentus.* Plants derived from hybridization with *H. pumilus* and *H. niveus* died as seedlings.

20. Helianthus ciliaris DC. Prod. 5:587. 1836. (T.: Mexico: Tamaulipas, *Berlandier 2118*, G-DC, photo F, IND, US!)

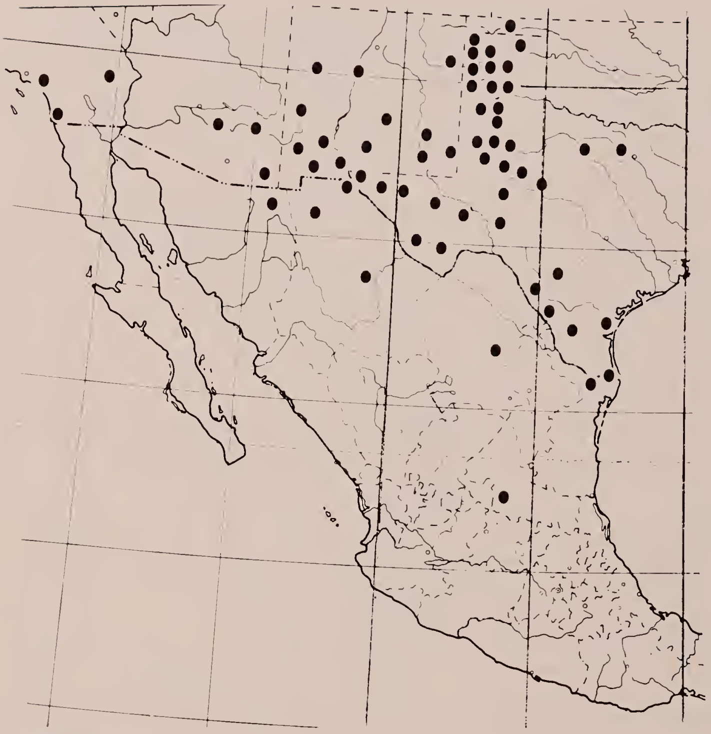
Linsecomia glauca Buckl. Proc. Phil. Acad. 13:458. 1861. (T.: Texas, McCullough Co., *Buckley*, PA)

Stems 0.4-0.7 m. tall, glabrous and glaucous or with a few scattered hairs; leaves mostly opposite, linear and 1-nerved to broadly lanceolate and 3-nerved, entire to serrate or shallowly lobed, and usually undulate, glaucous and glabrous to sparingly hispid or strumose-hispid, margins sometimes ciliate, bluish-green, 3.0-7.5 cm. long, 0.5-2.2 cm. wide; heads 1-few; disks 1.2-2.0 (-2.5) cm. in diam.; phyllaries ovate or oblong, obtuse to acute or abruptly mucronulate, appressed, somewhat graduate, ciliate, glabrous to sparingly puberulent on backs, shorter than disk, 2.0-3.5 mm. wide; rays 10-18, ca. 1 cm. long, rarely quite reduced or lacking; lobes of disk-corolla red; pales entire or shallowly 3-cuspidate, obtuse to acute, pubescent at tip; pappus of two ovate scales; achenes ca. 3 mm. long.

Chromosome number: n = 34 (51)

Distribution: in dry to damp, usually alkaline soils, Oklahoma and western Texas to southern Arizona and northern Mexico, to 8600 feet. June-Oct.

Helianthus laciniatus is readily distinguished from *H. ciliaris* on the basis of the characters given in the key but the confusion between the two in the



Map 20. *Helianthus ciliaris*

past is understandable. In the key the separation of *H. ciliaris* from *H. arizonensis* is based partly on disk flower color; however, one population is known from Catron Co., New Mexico (*Heiser 4704*) in which individuals with both colors occur. Unfortunately, no chromosome counts were secured, so it is not known if this is a mixed population of the two species, or if the yellow flowered individuals should be referred to *H. ciliaris*. If the disk color difference is not consistent it becomes very difficult to distinguish the two. *H. arizonensis* is a very short plant with relatively long, narrow phyllaries but individuals of *H. ciliaris* are known which may overlap it in these characteristics.

Because of its extensive system of creeping roots and vegetative multiplication, *H. ciliaris* or "blueweed", as it is sometimes called, can prove to be an obnoxious weed. The photograph presented by Robbins *et al* (1941) as *H. ciliaris* looks very much like *H. laciniatus*. In this work *H. ciliaris* is cited as established in five counties but there are no voucher specimens for three of them, San Luis Obispo, Ventura and Los Angeles.

Attempts to cross both 4n and 6n representatives of *H. ciliaris* with other species of the same chromosome level have proven unsuccessful.

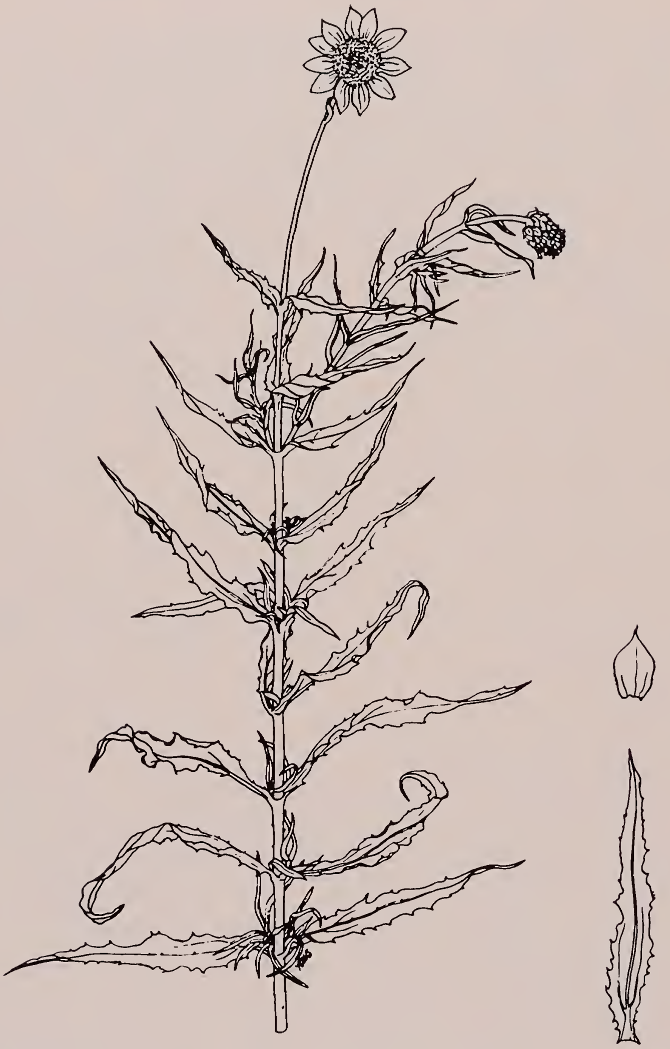


Fig. 20. *Helianthus ciliaris*

Jackson (1963) has suggested that *H. ciliaris* may have originated from hybrids of *H. arizonensis* and *H. laciniatus* and I can suggest no more likely origin, although the putative parents do not come into contact today so far as is known, and the artificial F_1 diploid hybrid between them does not resemble *H. ciliaris.*

Section III. Divaricati

Perennials from rhizomes, tubers or crown buds; disk corollas with yellow lobes except for seven species (see key below); leaves most frequently lanceolate to lance-ovate; primarily eastern and central United States and Canada.

Key to Series and Some Species of Section Divaricati

- Disk flowers entirely yellow
  - Rhizomes elongate, frequently over 15 cm. long; crown buds usually lacking
    - Leaves mostly or all opposite, not undulate, mostly broadly lanceolate to nearly ovate; plants sometimes tuber bearing........................1. Divaricati
    - Leaves mostly alternate, undulate..............................45. *H. floridanus*
  - Rhizomes short, usually much less than 15 cm. long, or lacking; crown buds often present
    - Rhizomes stout; main roots coarse, sometimes tuberous; leaves mostly lanceolate or narrower, mostly alternate; disks mostly medium sized (generally 1.3-2.0 cm.); stems glabrous or pubescent
      - Leaves short petiolate or rarely subsessile, widespread but rare in extreme southeast..2. Gigantei
      - Leaves subsessile, Fla. to La................................44. *H. simulans*
    - Rhizomes poorly developed or lacking; roots fibrous to coarse, never tuberous; stems glabrous
      - Disks small (generally 0.5-1.5 cm.); stem leaves well developed, narrowly lanceolate to ovate, opposite to middle of stem or above then becoming alternate; basal rosettes usually absent........................3. Microcephali
      - Disks small to large; leaves linear or nearly so; basal rosettes present
        - Disks over 1.5 cm., Fla...................................50. *H. carnosus*
        - Disks less than 1.5 cm., N.C., Ga., and Alab.............42. *H. longifolius*
- Disk flowers with red or purple lobes
  - Phyllaries linear-lanceolate to lanceolate, 1.0-2.0 (-2.5) mm. broad; stem leaves usually numerous and not conspicuously decreasing in size upward, sessile or subsessile, linear to nearly ovate, mostly alternate
    - Stems glabrous; roots stout, coarse; rhizomes short and stout; leaves flat ....34. *H. salicifolius*
    - Stems pubescent; roots fibrous to coarse; rhizomes either elongate, poorly developed or entirely lacking; leaves often revolute or undulate......4. Angustifolii
  - Phyllaries lanceolate to ovate or oblong, (2.0-) 2.5 mm. or more broad; stem leaves few to many, usually conspicuously decreasing in size upwards, if linear then opposite, or if ovate short to long petiolate

Rhizomes lacking; stems somewhat scapose, or if leafy with orbicular, scabrous leaves or lanceolate to rhombic ovate and somewhat hirsute below....5. Atrorubentes

Rhizomes well developed; cauline leaves lanceolate to rhombic ovate and scabrous..29. *H. rigidus*

Series 1. Divaricati

Roots fibrous to coarse, not tuberous; rhizomes usually long (15 cm. or more) and slender, sometimes becoming terminally enlarged; leaves mostly or all opposite, most frequently lance-ovate and 3-nerved; stem leaves well developed except in *H. occidentalis* and sometimes in *N. rigidus*; disks small to large; lobes of disk corolla always yellow, except in *H. rigidus*; achenes 3-6 mm. long.

Key to Species of Series Divaricati

Phyllaries conspicuously graduated and imbricate, usually tightly appressed, all or at least the outer shorter than disk; upper leaves usually conspicuously reduced in size.

- Phyllaries 2-3 mm. wide; stem leaves greatly reduced; disk flowers with yellow lobes..22. *H. occidentalis*
- Phyllaries 3-5 mm. wide; stem leaves gradually reduced; disk flowers usually with red lobes..29. *H. rigidus*

Phyllaries not conspicuously graduated and imbricate, frequently loose or spreading, equalling or exceeding disk; upper leaves not conspicuously reduced in size.

- Leaves sessile or nearly so
  - Stem, lower leaf surface and phyllaries densely white villous; leaves usually cordate-clasping..21. *H. mollis*
  - Stems, lower leaf surface and phyllaries glabrous, hispid to scabrous, or somewhat hirsute; leaves not cordate clasping (except occasionally in *H. divaricatus)*
    - Leaves strongly glaucous below..............................26. *H. eggertii*
    - Leaves not glaucous
      - Point of divergence of lateral leaf vein about 2.0 mm. from petiole base, blades subcordate to rounded at base; leaves all opposite..23. *H. divaricatus*
      - Point of divergence of lateral leaf vein more than 2.0 mm. from petiole base, blades mostly obtuse or cuneate at base; leaves sometimes alternate above..................................24. *H. hirsutus*
- Leaves definitely petiolate
  - Stems and leaves both pubescent, from densely hirsute to moderately scabrous
    - Leaves usually hirsute beneath, rusty or greenish in color; rhizomes rarely tuber bearing; leaves usually nearly all opposite..........24. *H. hirsutus*
    - Leaves puberulent, hirsutulous or tomentulose beneath, frequently whitish; rhizomes usually tuber bearing; leaves often alternate in upper 1/3 of plant..28. *H. tuberosus*

Stems essentially glabrous, rarely remotely scabrous; leaves pubescent or glabrous beneath

Leaves moderately serrate to entire, usually rather short-petiolate, mostly opposite; phyllaries equalling to slightly exceeding disk, never leaf-like..27. *H. strumosus*

Leaves deeply to moderately serrate, long petiolate, usually alternate above; phyllaries conspicuously longer than disk, often leaf-like.......25. *H. decapetalus*

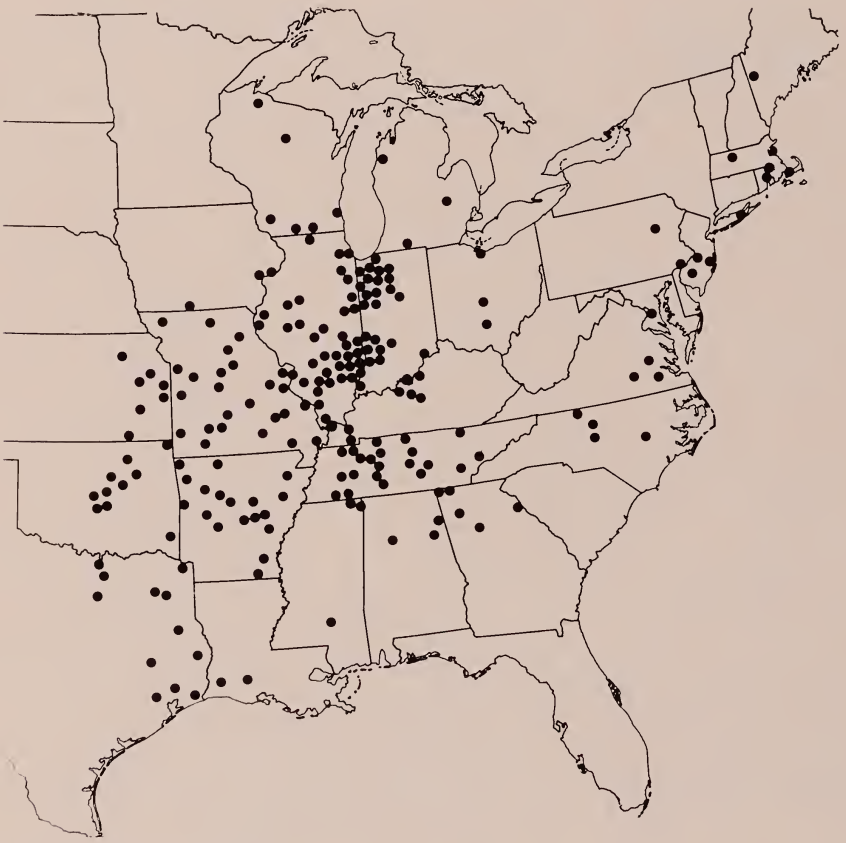
21. Helianthus mollis Lam. Encyc. 3:85. 1789. (T.: P. photo IND!)

H. pubescens Vahl. Symb. 2:92. 1791.

H. canescens Michx. Fl. Am. Bor. 2:40. 1803. (T.: P. photo GH!)

H. mollis var. *cordatus* S. Wats. Gard. For. 2:136. fig. 100. 1889. (T.: "cult. Arnold Arboretum, seed from N. T. Kidder, probably from Ariz. or N.M.", GH!)

H. mollis f. *flavida* Steyerm. Rhodora 55:108. 1953. (T.: Mo., Shelby Co. *Steyermark 70126* C!)



Map 21. *Helianthus mollis*

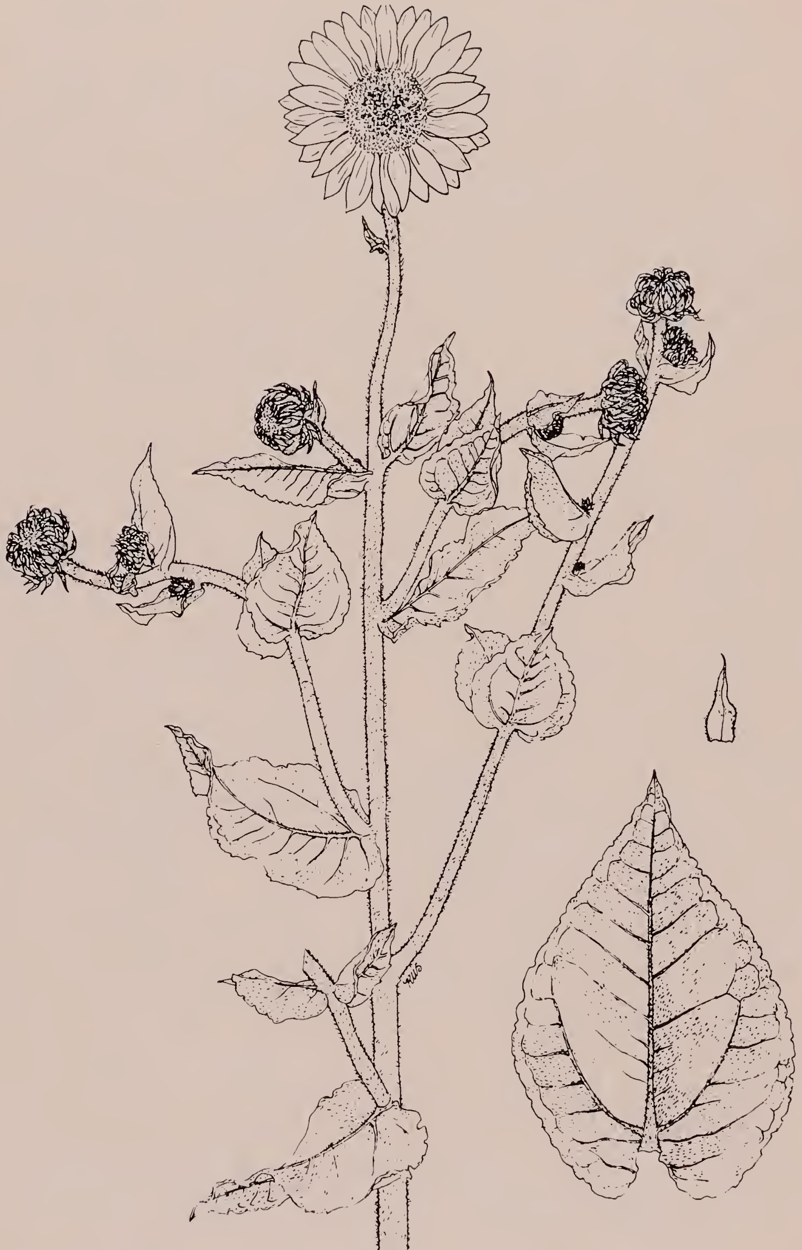


Fig. 21. *Helianthus mollis*

Rhizomes stout; plants usually colonial; stems 0.5-1.2 m. tall, hirsute to villous, unbranched or with short nearly erect branches; leaves all opposite, or sometimes becoming alternate near inflorescence, ovate to ovate-lanceolate or oblong, acute to acuminate, rounded to subcordate at base, sessile or sometimes clasping, entire or serrulate, densely cinereous-hispid to tomentose, more densely so below, ashy or gray-green, 6-15 cm. long, 2-8 cm. wide; heads sometimes solitary or more frequently in racemose or spiciform arrangement on short stout peduncles; disks 1.8-2.8 cm. in diam.; phyllaries many, linear-lanceolate to lanceolate, 2-4 mm. wide, acute to attenuate, equalling or slightly exceeding disk, tightly appressed in lower part, somewhat spreading above, densely hispid to villous or tomentose and sometimes glandular; rays 15-30, to 3 cm. long, light to bright yellow; disk corollas with lobes and base pubescent, pale to deep yellow; chaff linear, entire, tip villous; achene villous at apex, becoming glabrous, ca. 4 mm. long.

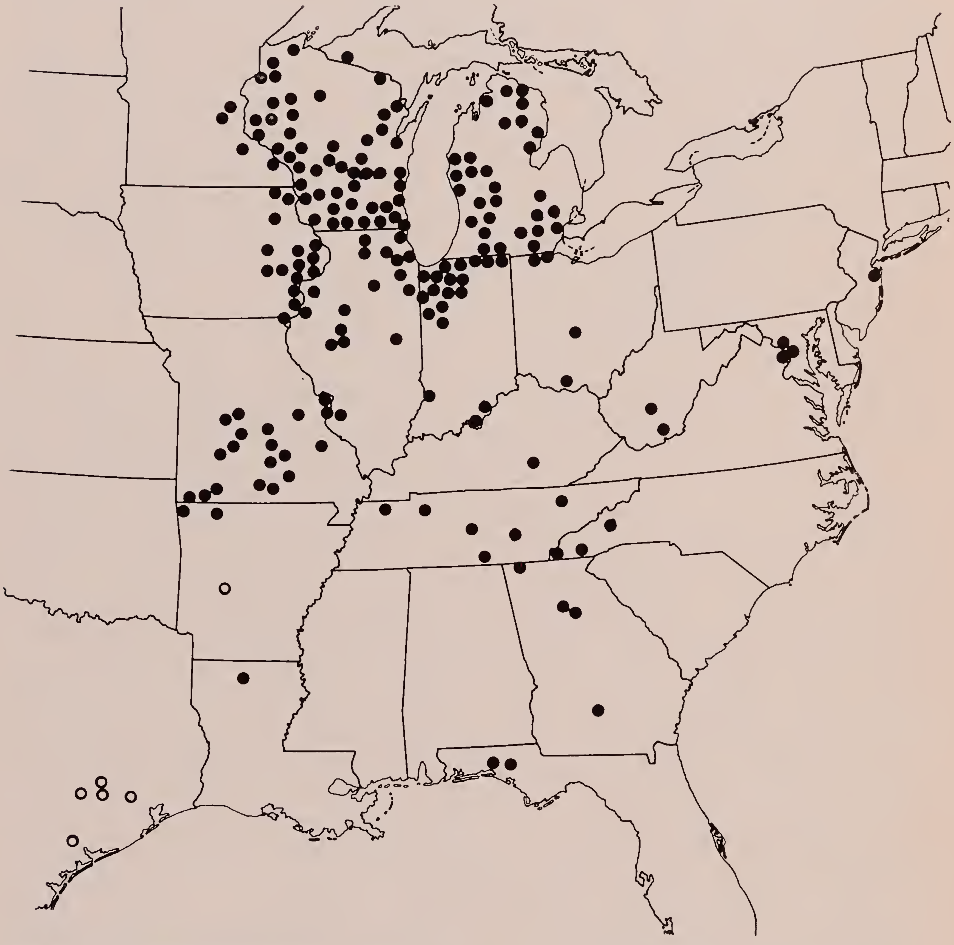
Chromosome number: n = 17

Distribution: Dry, usually open places, New England (introduced) to Wisc., south to northern Georgia and eastern Texas. Late July-Sept.

This is certainly one of the most distinctive sunflowers among the eastern perennials, and on morphological grounds, it does not appear particularly related to any other species, although it hybridizes readily with several of them. It is perhaps most nearly related to *H. occidentalis*, but this is not a close relationship. There is also a remote similarity to *H. tomentosus*, and it is possible that a mollis-like plant is involved in the ancestry of this hexaploid. The usually clasping leaves, the numerous phyllaries spreading at their tips, the numerous rays, and the dense pubescence give it a unique appearance among sunflowers. Although a given plant of the species can readily be recognized, it is far from being uniform morphologically. This is particularly true of height, disk diameter, leaf shape and amount of pubescence. There is abundant evidence of natural hybridization with other species; and although critical evidence is lacking, it is possible that introgression could be responsible for some of the variation. Environmental modification is also probably involved, and it is probable that *H. mollis* var. *cordatus* is a fairly typical *H. mollis* grown in good soil. That this variety comes from New Mexico or Arizona as stated in the description seems unlikely in view of the known distribution.

Natural hybrids are known with *atrorubens* (Beatley, 1963), *divaricatus*, *giganteus* (= *H. doronicoides*, *H. pilosus* Tausch?) *grosseserratus*, *occidentalis* (= *H. cinereus*), and *silphioides*. Artificial hybrids have been secured with *atrorubens*, *decapetalus* (2n), *divaricatus*, *giganteus*, *grosseserratus*, *longifolius*, *maximiliani*, *microcephalus*, and *occidentalis*.

22. Helianthus occidentalis Riddell, Suppl. Cat. Ohio. Pl. 13. 1836. (Type loc. Ohio, Tuscarawas Co.; Neotype: Ohio, Franklin Co., Georgesville, *Wm. C. Werner,* 29 Aug. 1892, OSU! dupls. at IND, NY)



Map 22. *Helianthus occidentalis.* Solid dots, ssp. *occidentalis*; open circles, ssp. *plantagineus*

Rhizomes slender; stolons frequently present, giving rise to new rosettes in late summer; stems 0.6-1.5 m. tall, slender, densely pilose to hirsute at base, less so to nearly glabrous above, often red, leaves mostly near base, rarely well-developed on stems, oblong-lanceolate to ovate, entire to serrulate or rarely serrate, scabrous to pilose, 5-20 (-31) cm. long, 1.5-7.0 (-10.0) cm. wide, petioles frequently as long as or sometimes longer than blades, sometimes slenderly winged; stem leaves opposite, few, usually much reduced, becoming

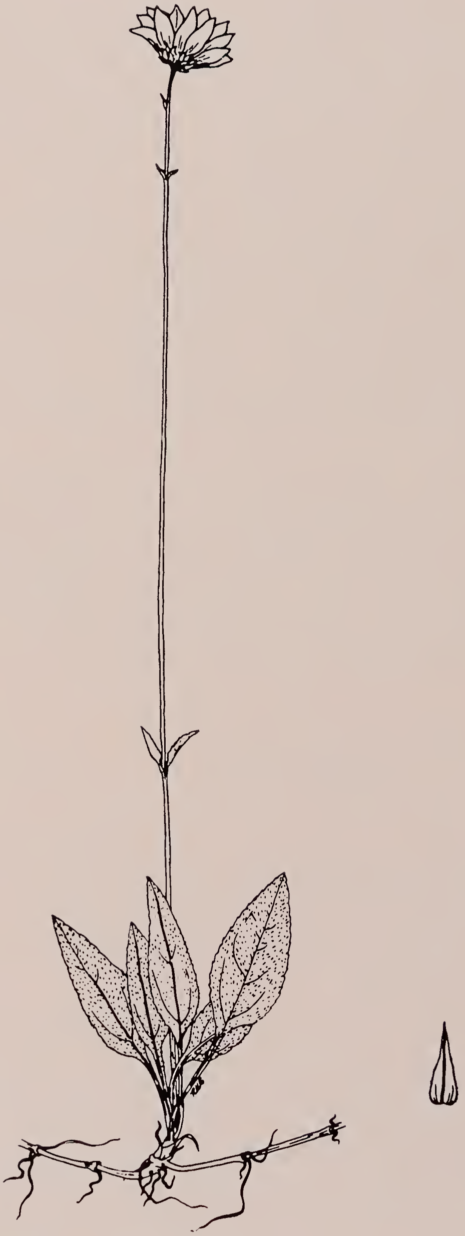


Fig. 22. *Helianthus occidentalis*

bract-like; heads usually few on long peduncles; disks 0.9-1.4 cm. in diam.; phyllaries somewhat imbricate, lanceolate to lance-ovate, acute to acuminate, 2-3 mm. wide, slightly shorter than disks to rarely slightly exceeding disks, nearly glabrous, or sparingly pilose and ciliate; rays usually deep yellow, generally 10-15, to about 2 cm. long; pales subtricuspidate, nearly glabrous at tips; achene sparingly villous, becoming glabrous, 3-4 mm. long.

This species is very well marked, but its relationships are not at all clear-cut. The scapose-like aspect suggests an affinity with the southeastern group, perhaps *H. atrorubens*, whereas the long rhizomes suggest relationship with the eastern perennials, perhaps *H. mollis* with which it is known to hybridize frequently. This species reaches its greatest abundance in the glaciated regions of the northcentral states and becomes rather local in the southeast.

Curtis and Cottam (1950) have reported an antibiotic and autotoxic effect in this species.

Watson (1929) has remarked on the extreme variability of *H. occidentalis*. Plants grown by us in the garden in fertilized soil reach heights of 2 meters, have huge leaves, and are much branched with numerous heads. The same plants a year later assumed a much more "normal appearance." Therefore, it is probable that some of the variation is due to environmental modification of the phenotype. Two subspecies, which apparently have a genetic basis, however, may be recognized.

Key to Subspecies

Leaves rough to the touch, entire to subentire. . . . . *H. occidentalis* ssp. *occidentalis*
Leaves smooth to the touch, usually serrate. . . . . *H. occidentalis* ssp. *plantagineus*

22a Helianthus occidentalis ssp. occidentalis

H. dowellianus M. A. Curtis, Amer. Jour. Sci. Art. 44:82. 1843. (T.: North Carolina, Macon Co., *Curtis*, NY?)
H. occidentalis var. *dowellianus* T. & G. Fl. N. Amer. 2:504. 1843.
H. illinoensis Gleason, Ohio Nat. 5:214. 1904. (T.: Illinois, Alexander Co., *Gleason*, MO!)
H. occidentalis var. *illinoenesis* Gates, Bull. Torrey. Club. 37:79. 1910.
H. occidentalis var. *occidentalis* Cronquist, Rhodora 47:399. 1945.

Leaves scabrous, usually entire or subentire; phyllaries equalling disk or shorter, pubescent to glabrous.

Chromosome number: n = 17

Distribution: Dry often sandy soils, Wisconsin to eastern North Dakota, south to Florida and Louisiana. July-Sept., mostly August.

At least two problems remain unresolved in this subspecies. One of these is the proper disposition of *H. dowellianus*. Although Watson (1929) states the type is at New York it could not be located. However, the description and other collections indicate that this is a plant one to two meters tall, much branched, with quite large leaves which are well developed on the stems. Such plants appear very similar to artificial hybrids of this species with *H. atrorubens* and might well owe their origin to hybridization with that species. The other possibility is that they are simply plants from fertile habitats and represent ecological modifications.

The second problem concerns those plants of this subspecies which have few basal leaves but several pairs of well developed cauline leaves. Such plants are found locally in the Appalachian region from Maryland to Georgia. They apparently are included under the concept of "dowellianus" in recent eastern floras. It might be possible that they owe their origin to introgression from some other species but it is difficult to postulate the species that might be responsible. Thus, there is the possibility that they are a distinct regional race of this species. If this is true, then they may be worthy of some taxonomic recognition.

As stated above, *H. dowellianus* may be a hybrid of this subspecies with *H. atrorubens*. Natural hybrids are rather common with *H. mollis*. *H. cinereus* var. *Sullivantii* T. & G. (Fl. N. Am. 324. 1842. T.: Ohio, Columbus, *Sullivant* GH!) is apparently this hybrid. Other natural hybrids are known with *divaricatus*, *giganteus*, *grosseserratus*, *longifolius*, and perhaps *angustifolius*. Artificial hybrids have been secured with *atrorubens*, *grosseserratus*, *longifolius*, and *maximiliani*.

22b Helianthus occidentalis ssp. plantagineus (T. & G.), *stat. nov.*

H. occidentalis var. *plantagineus* T. & G. Fl. N. Am. 323. 1842. (T.: Texas, *Drummund*, NY!)
H. plantagineus E. E. Wats. Pap. Mich. Acad. Sci. 9:367. 1929.

Leaves appressed pubescent, usually serrate; phyllaries glabrous, equalling or exceeding disk.

Chromosome number: Unknown

Distribution: Southeastern Texas and Garland Co., Arkansas.

Although differing only slightly from the typical subspecies, this race shows a distinct geographical position, hence, is probably deserving of subspecific recognition. Watson (1929) also records this species from Mexico, probably on the basis of *Parry 470* (NY) labeled "Mexico, en route from San Luis Potosi to San Antonio, Texas."

The *H. cinereus* of Torrey and Gray, as Gray, himself, later recognized, is probably a hybrid involving this subspecies of *H. occidentalis* with the other parent most likely being *H. mollis*.

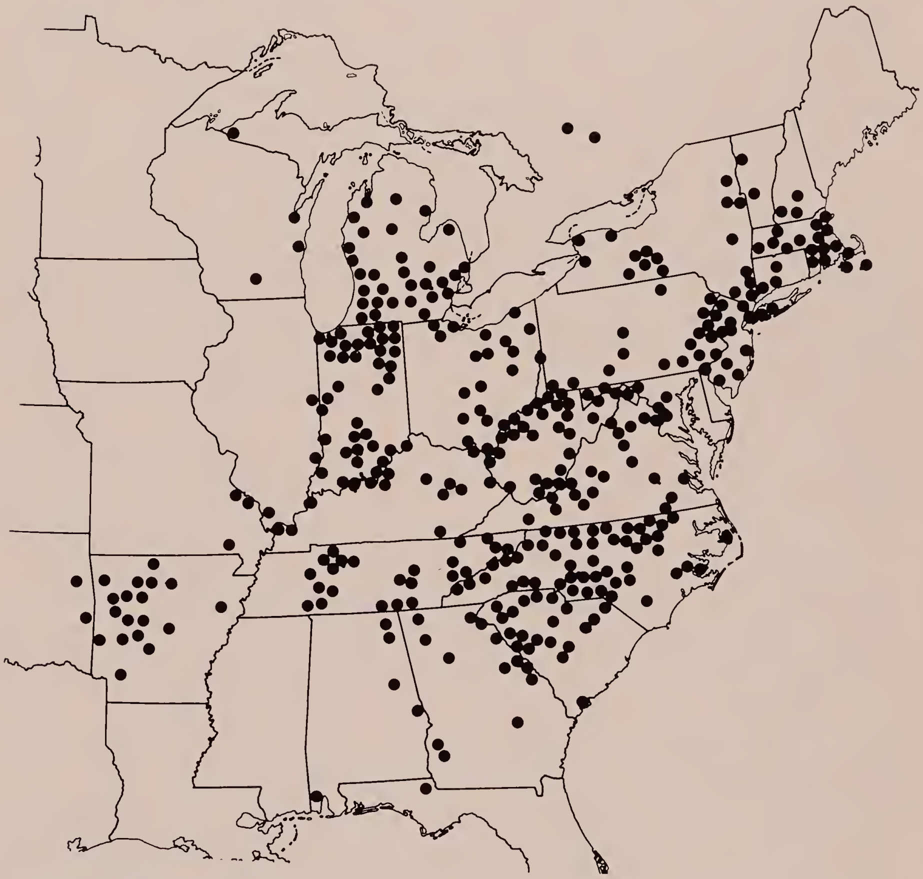
23. Helianthus divaricatus L. Sp. Pl. 906. 1753. (T.: LH, Photo, GH!)

H. truncatus Schwein. ex Ell. Sketch. 2:416. 1824. (T.: Salem, North Carolina, *Schweinitz*)

H. divaricatus var. *angustifolius* O. Ktze. Rev. Gen. 1:343. 1891. (T.: New York, Niagara Co., *Kuntze*, NY!)

H. divaricatus var. *latifolius* O. Ktze. l.c. (T.: New York, *Kuntze*, NY!)

H. divaricatus var. *ternatus* Farwell, Rep. Mich. Acad. Sci. 22: 185. 1921. (T.: Mich. Washtenaw Co., *Farwell 5248*, BHM!)



Map 23. *Helianthus divaricatus*

Rhizomes abundant, slender, slightly thickened at tips; stems 0.5-1.5 m. tall, slender, simple or branched at summit, glabrous, or rarely somewhat hispid-hirsute, often glaucous; leaves rather thick, opposite, horizontally divergent, narrowly lanceolate, or more often triangular-ovate or -lanceolate, tapering from subcordate to truncate sessile or sub-sessile base to acuminate tip, lateral veins diverging from near base of leaf, scabrous above, sparsely hispid to hispidulous beneath, subentire to serrate, 6.0-15.0 cm. long, 1.0-5.0 cm. wide; heads 1-several at tips of cymose stiffly divergent branches; disk 1.0-1.5 cm. in diam.; phyllaries slightly reflexed, linear-lanceolate, attenuate, nearly glabrous to hispidulous, 2-3 mm. wide, equalling or slightly exceeding disk in length; rays 8-12 (-15), 1.5-3.0 cm. long, rather narrow; pales 3-cuspidate, middle cusp acuminate, slightly pubescent; achene glabrous, ca. 3 mm. long.

Chromosome number: n = 17

Distribution: In dry, usually open habitats from southern Quebec to Wisconsin, south to north Florida and Oklahoma. July-Sept.

This species is the earliest blooming perennial in eastern North America. It is also one of the most common in this region and its range overlaps that of a great number of species. Consequently, numerous opportunities for hybridization exist, and a large number of hybrids have been reported. The most likely explanation for the unusual specimen of this species reported by Watson (1929, his *530* from Albemarle, North Carolina) is that it is a hybrid with *H. atrorubens*. Smith found the two species growing together at this locality in 1956, although no hybrids were found. Gray (1884) suspected that *H. giganteus* var. *ambiguus* was a hybrid between *H. divaricatus* and *H. giganteus*. This hybrid is fairly common as is the one with *H. grosseserratus*. These last two hybrids are rather similar in appearance but the one involving *H. grosseserratus* usually has a glabrous stem. The hybrid with *H. microcephalus* is also fairly common and has been the subject of a detailed study by Smith and Guard (1958). Hybrids with both *H. mollis* and *H. occidentalis* have been reported from northern Indiana (Jackson and Guard, 1957); and *H. divaricatus* x *mollis* also is known from McDonald Co., Missouri (*Bush 5035*, MO, NY; *E. J. Palmer*, Aug. 9, 1902, IND, MO). One specimen has been seen which may be a hybrid with *H. salicifolius* (Ark., Logan Co., *Demaree 16033*, MO).

Despite the rather extensive hybridization, this species is remarkably constant throughout most of its range. The most conspicuous variants are found along the eastern seaboard and in the Ozark Plateau. The eastern plants, the variety *angustifolius* of Kuntze, are generally small, with slender, usually unbranched stems and very narrow lanceolate leaves. Whether these plants constitute an environmental modification of the phenotype or a genetic race has not been determined, although one occasionally encounters depauperate individuals on poor sites in other parts of the range which are similar to the eastern plants. For example, a specimen in flower collected in Monroe Co., Indiana (*Smith 1034*) was about 2 dm. tall, monocephalic, with very narrow leaves. Rhizomes of this plant were transferred to the

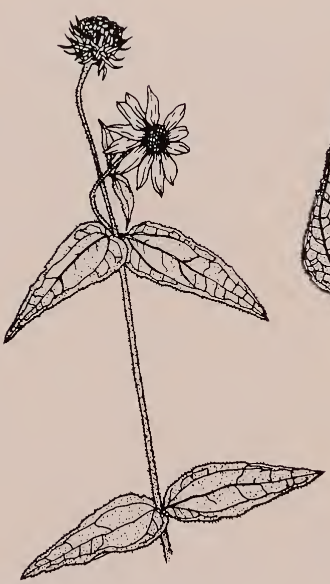


Fig. 23. *Helianthus divaricatus* (Ozark race)

experimental garden, and the following summer the plant reached 1.5 m. tall in height and bore broad leaves, branches at every node, and numerous heads.

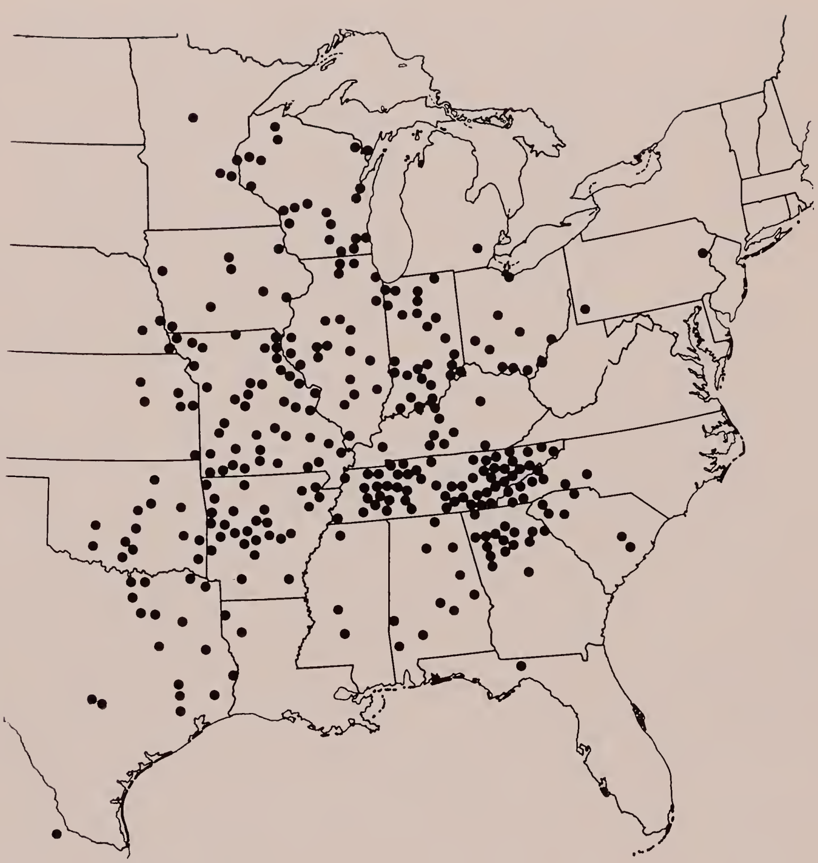
The chief distinguishing features of the Ozark plants (which is shown in the illustration) are more pubescent stems and leaves, and more numerous ray flowers and phyllaries. Putative backcross and F_2 individuals from hybrid swarms of *H. divaricatus* x *mollis* resemble some herbarium specimens of *H. divaricatus* from Arkansas and Oklahoma, thus the possibility that introgression from *H. mollis* has occurred in the Ozarks deserves detailed study. An examination of the map reveals that the Ozark plants also form a very discrete geographical phase of the species, apparently isolated from the remainder of the species. Thus, it is also possible that the morphological differences of these plants may stem simply from differentiation that occurred when a segment of this species became effectively geographically isolated from the remainder. The morphological differences and the geographical distributions seem to warrant subspecific recognition of the Ozark populations, but such status must wait until more detailed field work has been undertaken.

Helianthus divaricatus does not appear to have a particularly close relationship with any of the other diploid species, and morphologically, it is nearest to certain tetraploid members of *H. strumosus* and *H. hirsutus*. It seems very likely that it has contributed a genome to these species. At times, it is extremely difficult to distinguish *H. divaricatus* from these tetraploids, although they are apparently very effectively genetically isolated. No one character will always serve to distinguish *H. divaricatus* from these tetraploids but in general it is found that the tetraploids have: (1) somewhat larger over-all size of heads, leaves, and stems, (2) larger pollen grains (ca. 30 microns) and guard cells, and (3) usually a petiole at least 5 mm. long. It should be pointed out, however, that many of the hybrids of *H. divaricatus* with other diploids also have short petioles.

Artificial hybrids of *H. divaricatus* have been secured with *H. decapetalus* (2n), *H. giganteus*, *H. grosseserratus*, *H. microcephalus*, and *H. mollis*. Seed have been secured in crosses with *H. hirsutus* and *H. tuberosus*, but these failed to germinate.

24. Helianthus hirsutus Raf. Ann. Nat., p. 14, 1820. (T.: Ky., *Rafinesque* NY?)

H. diversifolius Ell. Sketch 2:423. 1824.
H. hispidulus Ell. Sketch 2:419. 1824.
H. hirsutus var. *diversifolius* T. & G. Fl. N. Am. 2:329. 1842.
H. hirsutus var. *trachyphyllus* T. & G. *l.c.* (T.: Ark. *Pitcher* NY!)
H. hirsutus var. *stenophyllus* T. & G. *l.c.* (T.: Western Louisiana, *Hale*, NY!)



Map 24. *Helianthus hirsutus*

H. strumosus var. *leptophyllus* T. & G. *l.c.* (T.: Louisiana, Tammany Parish, *Drummond* NY!)

Viguiera leptocaulia S. Wats. Proc. Am. Acad. 26:140. 1891. (T.: Mexico; Nuevo Leon *Pringle 2247* G!)

H. strumosus x *decapetalus* Holzinger, Contr. U.S. Natl. Herb. 1:194. 1892. (T.: Indian Territory (Okla.) *Sheldon 326* US!)

H. leptocaulis (S. Wats.) Blake, Proc. Am. Acad. 51:519. 1916.

H. chartaceus E. E. Wats. Papers Mich. Acad. Sci. 9:450. 1929. (T.: Nebr.: Cass Co., *Bates 5247* NEB!)

H. stenophyllus (T. & G.) E. E. Wats. *l.c.* 396.

H. virilis E. E. Wats. *l.c.* 451. (T.: Kans: Wyandotte Co., *Mackenzie 64398* KSC!)

H. vernalis E. E. Wats. *l.c.* 407. (T.: Missouri, Texas, *Reverchon 2582*, MO!)

Rhizomes abundant, slender, slightly thickened apically; stems 1.0-2.0 m. tall, relatively stout, simple or branched at summit, scabrous to densely hirsute; leaves mostly opposite, occasionally alternate above, somewhat divaricate to ascending, narrowly lanceolate or more commonly ovate, occasionally broadly so, rounded or tapering to short petiole 0.5-2.0 cm. long, tip acuminate, triple-veined, the lateral veins diverging 0.5-2.0 cm. from leaf base, scabrous to hirsute above, hirsute below, subentire to serrate, 7.0-18.0 cm. long and 1.0-8.0 cm. wide; heads 1-several at ends of usually short, thick peduncles; disk 1.2-2.5 cm. in diam.; phyllaries tight, rarely somewhat reflexed, equalling or slightly exceeding disk, 2.0-3.0 (-3.5) mm. wide, linear-lanceolate, attenuate; rays 10-15, ca. 2.0 cm. long, chaff shallowly 3-cuspidate, pubescent on tip and keel; achene 4.0-4.5 mm. long.

Chromosome number: $n = 34$

Distribution: Common in rather dry, usually open habitats, Pennsylvania to Minnesota, south to Georgia and northern Nuevo Leon, Mexico. Mid-July to October.

Three major morphological phases of this species, differing slightly in leaf shape or pubescence, may be distinguished and were maintained as varieties by Fernald (1950).

Helianthus hirsutus var. *hirsutus,* which has long hirsute middle internodes and lower leaf surfaces, as opposed to the shorter more scabrous type of pubescence of the other varieties, is the common type in the eastern part of the range (Pennsylvania to Indiana, south to Georgia and Louisiana). Variety *trachyphyllus* with broadly lanceolate to ovate leaves is the dominant form in the western portion of the range, and variety *stenophyllus* with more narrowly lanceolate leaves is southern (Arkansas, Louisiana and Texas) although var. *trachyphyllus* also occurs in the same area. There might be some justification in recognizing var. *hirsutus* as one subspecies and varieties *trachyphyllus* and *stenophyllus* as a second; but in view of the fact that *H. hirsutus* is itself a borderline species, there seems little reason to make new ranks for these minor variants. For those who desire to use trinomials the present varietal classification will serve.

Of the diploid species, *H. divaricatus* is most similar morphologically to *H. hirsutus* and the usual absence of a petiole in the former is the best distinguishing feature. It seems likely that *H. divaricatus* has contributed one genome to *H. hirsutus.* Hybrids of *H. divaricatus* with both *H. giganteus* and *H. mollis* produce plants approaching *H. hirsutus* in appearance, and it is possible that one or both of these other species also is involved in the origin of *H. hirsutus.* It is, of course, possible that *H. hirsutus* had a single origin

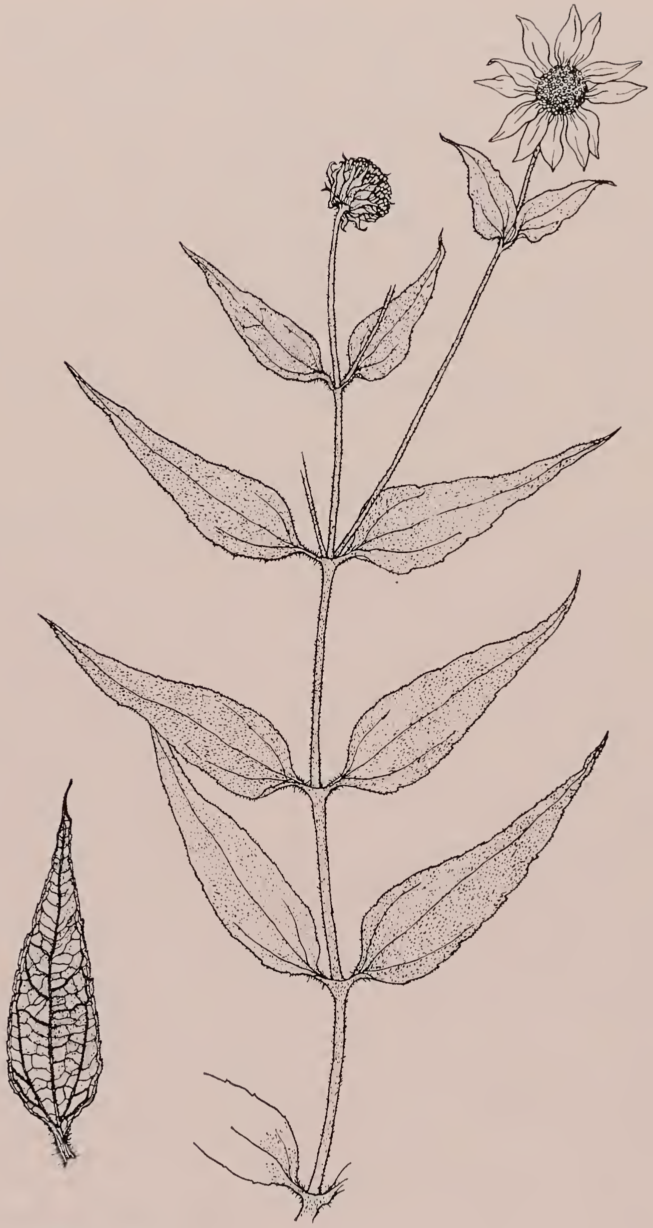


Fig. 24. *Helianthus hirsutus*

and that its present great variability is due to polyploid segregation or hybridization with other tetraploids or both.

Of the tetraploids, *H. strumosus* is certainly very closely related to *H. hirsutus,* if indeed they should be considered separate species. It might be desirable to combine the tetraploid members of *H. strumosus* with *H. hirsutus* to constitute a single species. Additional study is necessary before this problem can be resolved; so for the present, the traditional treatment is followed placing those plants with hirsute or densely scabrous stems in *H. hirsutus* and those with glabrous or nearly glabrous stems in *H. strumosus.*

The differences between *H. hirsutus* and *H. decapetalus,* the other tetraploid closely related (Smith, 1961) to it, are discussed under that species.

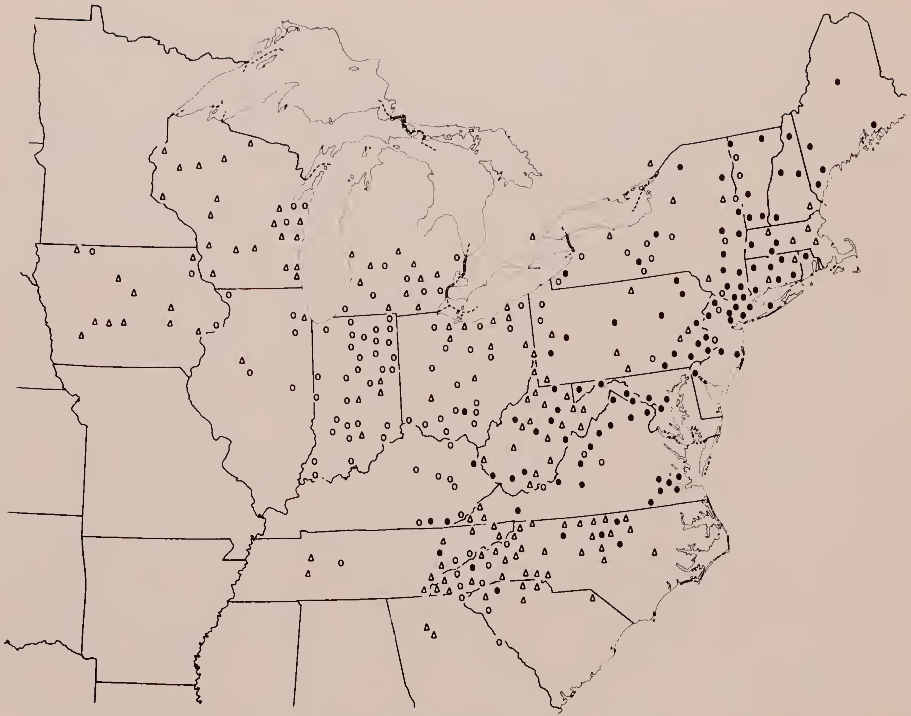
Rather highly fertile artificial hybrids of *H. hirsutus* have been secured with both tetraploid *H. strumosus* and *H. smithii.* As yet hybrids have not been secured with *H. decapetalus,* although one would expect that hybrids could be obtained since *H. decapetalus* crosses quite readily with 4n forms of both *H. strumosus* and *H. smithii.* Artificial hybrids are also known with *H. annuus* and *H. tuberosus.*

The type of this species is a collection by Rafinesque from Kentucky. Watson (1929) designated a Rafinesque collection from the New York Botanical Garden as the type but a recent search there failed to turn up this specimen.

25. Helianthus decapetalus L. Sp. Pl., 906. 1753. (T.: LH, photo GH!)

H. frondosus L. Amoen. Acad. 4:290. 1759.
H. trachelifolius Miller, Garden, Dict. Ed. 8. no. 7. 1768.
H. ramossissimus Miller, *l.c.* no. 8 (T.: BM, photo GH!)
H. prostratus Willd. Sp. Pl. Ed. 4. 3:2242. 1800.
H. tenuifolius Ell. Sketch, 2:420. 1824.
H. decapetalus var. *frondosus* Wood, Class Book, Rev. Ed. 499. 1872.
H. decapetalus f. *frondosus* Voss. Vilmorin's Bliumengärt. Ed. 3. 1:483. 1894.
H. scrophulariifolius Britt. Man. 955. 1901. (T.: New Jersey, Camden Co., *Bicknell* Aug. 14, 1899 NY!)
H. decapetalus var. *scrophulariaefolius* House. Bull. N.Y. St. Mus. 243:70. 1923.

Rhizomes abundant, slender, rarely thickened apically; stems erect 0.6-2.0 m. tall, slender, usually with several branches, glabrous except near heads; leaves opposite below, usually becoming alternate at middle nodes or above, lanceolate to broadly ovate, rounded or long-tapering at base to a usually winged petiole 2.0-5.0 cm. long, acuminate at tip, shallowly serrate or more frequently deeply serrate, dark green and moderately to densely scabrous



Map 25. *Helianthus decapetalus.* Solid dots, probable diploids; open circles, probable tetraploids; triangles, not determined as to probable ploidy level.

above, light green and glabrous or sparingly scabrous-hispidulous beneath, the lateral veins frequently alternate, 7.0-18.0 cm long and 3.5-10.0 cm. wide; heads 1-several on slender, ascending peduncles; disk 1.2-2.5 cm. in diam.; rays 8-12, light yellow, to 2.5 cm. long; phyllaries loose, usually exceeding the height of disk by one-half their length, or more often longer and leafy, often reflexed, linear lanceolate, acuminate; achenes 3.5-5.0 mm. long.

Chromosome numbers: n = 17, 34

Distribution: shaded woodlands, usually in rich soil, rarely persisting in openings or cut-over woods, Maine to Iowa, south to northern Georgia. July-Aug.

This is the only "species" of *Helianthus*, thus far known, which comprises both diploids and tetraploids. Several attempts have been made to secure hybrids between the two chromosome races without success. Although the two are therefore apparently completely isolated genetically and hence good biological species, we have as yet found no completely satisfactory way to separate them by gross morphological characters. When grown together in

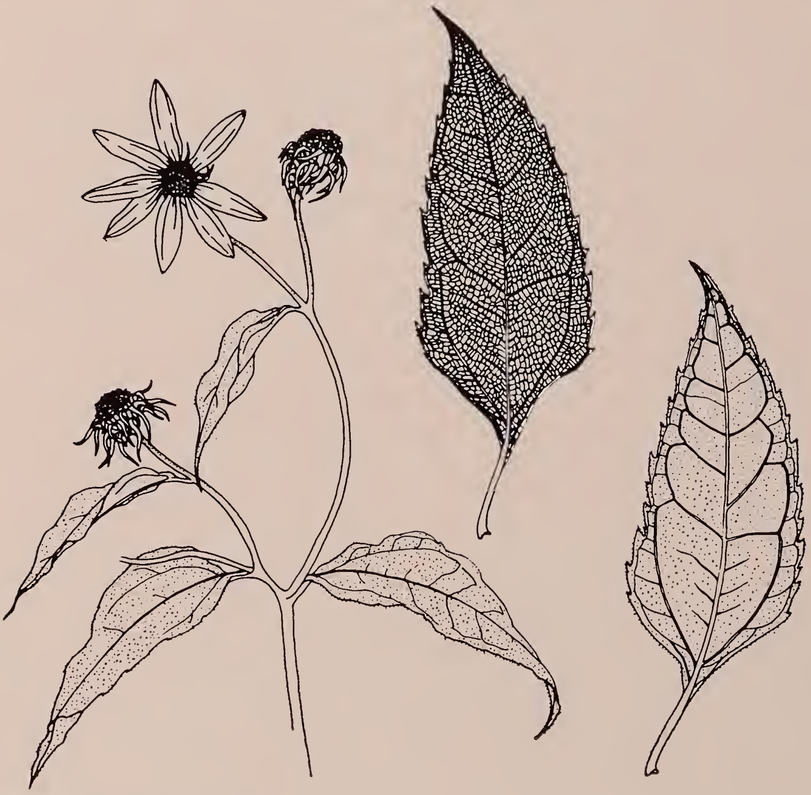


Fig. 25. *Helianthus decapetalus*

the experimental garden, the tetraploids generally are more robust, with broader leaves and slightly larger heads.

Smith (1960) reported the chromosome counts obtained for this species and discussed the possibility of the tetraploid being an autoploid. More recently he (unpubl.) has measured guard cell lengths of a large series of herbarium specimens and finds that the measurements fall into two classes with almost no overlap. The presumed diploids and tetraploids are plotted on the map of the species. It can be seen that, while there is some intermingling of the two, particularly in the Appalachian region, the presumed diploids are predominantly more eastern in their distribution than are the presumed tetraploids.

Helianthus decapetalus does not appear to be particularly closely related to other diploids of this series and is perhaps most similar to *H. glaucophyllus* and *H. microcephalus* among diploid species but at times it may intergrade with the tetraploids, *H. hirsutus* and *H. strumosus.* The more deeply serrate leaves with rather long petioles, the longer phyllaries, and the paler rays of *H. decapetalus* generally serve to distinguish it from these two species, and the nearly glabrous stem offers an additional character to separate it from *H. hirsutus.* A population of *H. hirsutus* from Monroe Co., Ind. (*Smith 1051*) had some plants showing characters of *H. decapetalus*, although the latter species was not found in the vicinity. Either polyploid segregation or past hybridization might be the explanation for the decapetalus-like features observed.

Artificial hybrids of diploid *H. decapetalus* have been obtained with *H. carnosus*, *H. divaricatus*, *H. giganteus* and *H. mollis.* At the tetraploid level hybrids have been secured with *H. laevigatus*, *H. smithii*, and *H. strumosus.*

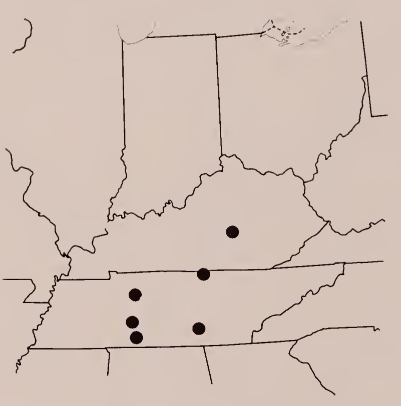
25a Helianthus x multiflorus L. (*H. annuus* x *decapetalus*)

H. multiflorus L. Sp. Pl. 2. 905. 1753. (T.: LH, photo GH!)
H. grandiflorus Juss. ex. Pers. Synop. 2:475. 1807.
H. decapetalus var. *multiflorus*? A. Gray, Syn. Fl. 1^2:280. 1884.
H. decapetalus f. *multiflorus* Voss, Vilmorin's Blumengärt. Ed.3. 483. 1894.

This sunflower is known only as a cultivated ornamental. Since it is a sterile triploid it is propagated solely by means of rhizomes. Morphologically it is rather similar to *H. decapetalus.* Both single-flowered and double-flowered forms are known, but only the double flowered form is common in cultivation in the United States today. Double-flowered plants may rarely appear among other perennial species, chiefly as the result of insect injury, and double-flowered cultivated forms of *H. annuus* are also known.

The evidence for considering this species a hybrid is presented by Heiser and Smith (1960) and additional discussion may be found in Heiser (1960a).

26. Helianthus eggertii Small. Flora S.E. U.S. 1267. 1903. (T.: Tenn., Dickson Co., *Eggert* in 1897, NY!)



Map 26. *Helianthus eggertii*

Stems purplish, glabrous and glaucous, 1-2 m. tall; leaves mostly or all opposite, uppermost sometimes alternate, lanceolate, acute to acuminate, and tapering to a sessile or subsessile base, obscurely 3-veined, glaucous and strumose above, strongly glaucous below, entire or serrulate, sometimes slightly revolute on drying, 9-15 cm. long, 2.0-3.5 cm. wide; heads few, disk 1.2-1.7 cm. in diam.; phyllaries lanceolate, 2-3 mm. wide, acuminate, equalling or slightly exceeding disk, mostly erect, glaucous, ciliolate on margins; rays 10-14, to 2 cm. long; disk flowers 5-6 mm. long; chaff entire or obscurely 3-cuspidate, middle cusp short, acute, ciliate; achene 5 mm. long.

Chromosome number: n = 51

Distribution: known only from barrens of central Tennessee and Lincoln Co., Kentucky. Late Aug.-early Sept.

This species, as Watson (1929) pointed out, is closely related to *H. laevigatus* and it is likely that *H. laevigatus* is involved in its parentage. It is difficult to postulate what diploid species might have crossed with *H. laevigatus* to give rise to *H. eggertii*, but of the extant species, *H. decapetalus* is the most likely candidate.

From *H. laevigatus*, *H. eggertii* is separated by its larger heads, more conspicuously strumose leaves, and the much larger rhizomes. It is also closely related to *H. strumosus*, which also may possess glaucous leaves although they are usually more distinctly petiolate. In fact, it is likely that certain specimens which are included in this species (Kentucky: Lincoln Co.,

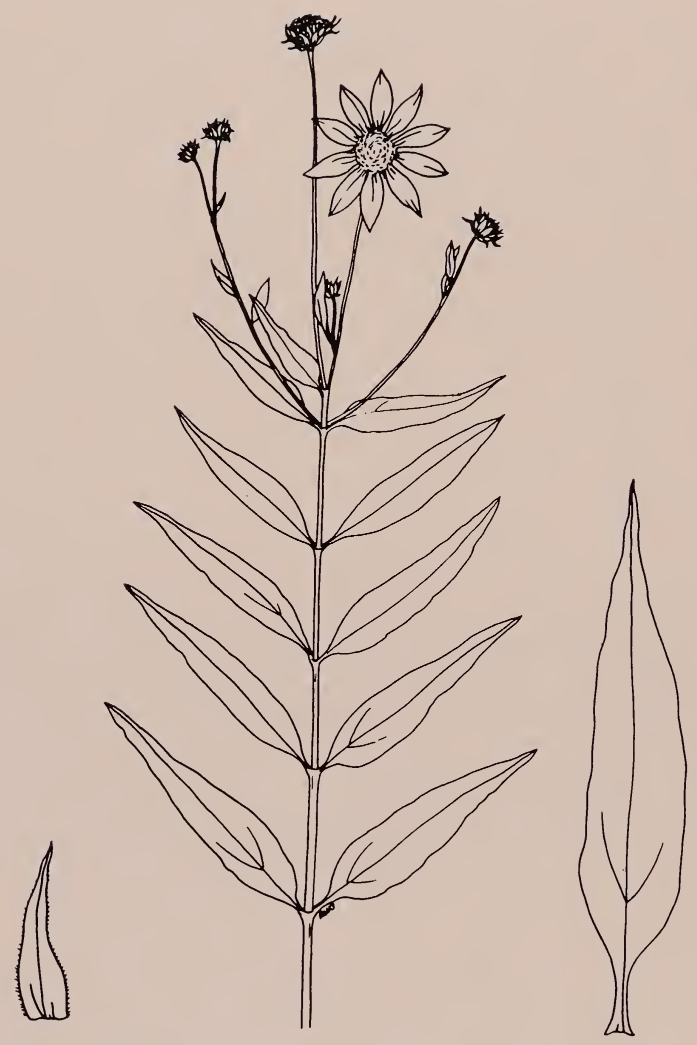


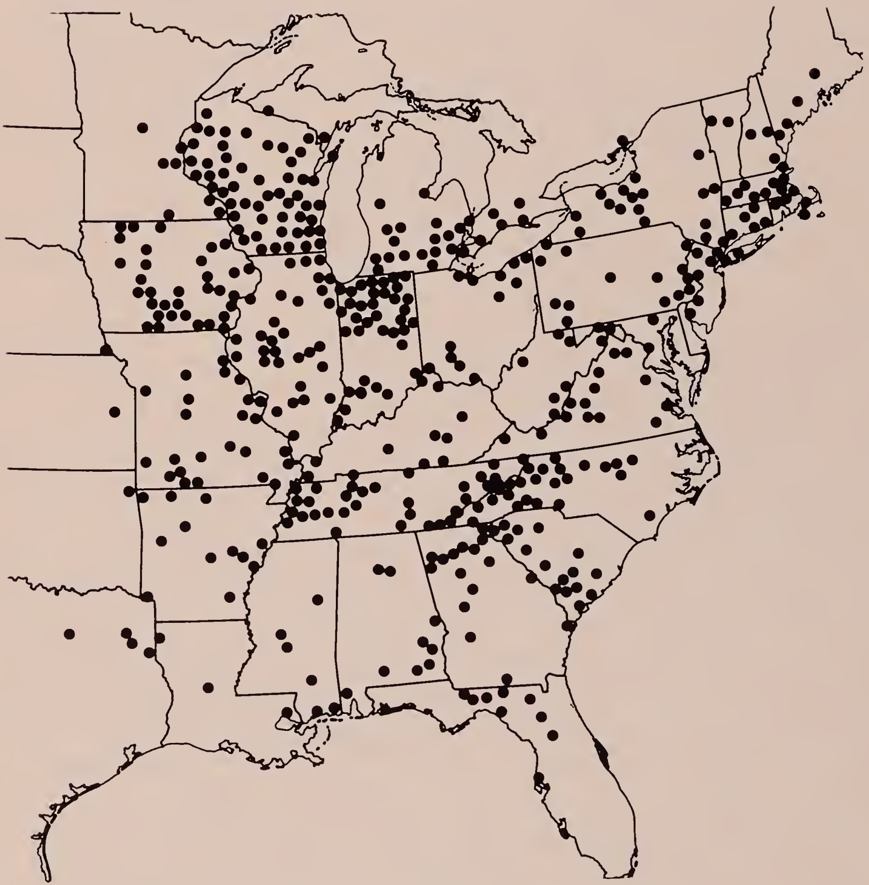
Fig. 26. *Helianthus eggertii*

Smith 1002; Tennessee: Trundy Co., *Beatley 22587a*, Clay Co., *Beatley 26787*, all at IND.) which show a short but definite petiole are hybrids with *H. strumosus*. A putative hybrid with *H. microcephalus* is also known; see under discussion of *H. microcephalus*.

Since we have not had this species in cultivation its crossing relationships are unknown; but on the basis of what is known of the other eastern sunflowers, one might predict that it would hybridize readily with the other hexaploids.

27. Helianthus strumosus L. Sp. Pl. 905. 1753. (T.: LH; Photo, GH!)

H. laevis Walt. Fl. Carol. 215. 1788.
H. macrophyllus Willd. Hort. Berol. t. 70. 1816.
H. striatus Raf. Atl. Jour. 1:17. 1832.



Map 27. *Helianthus strumosus*

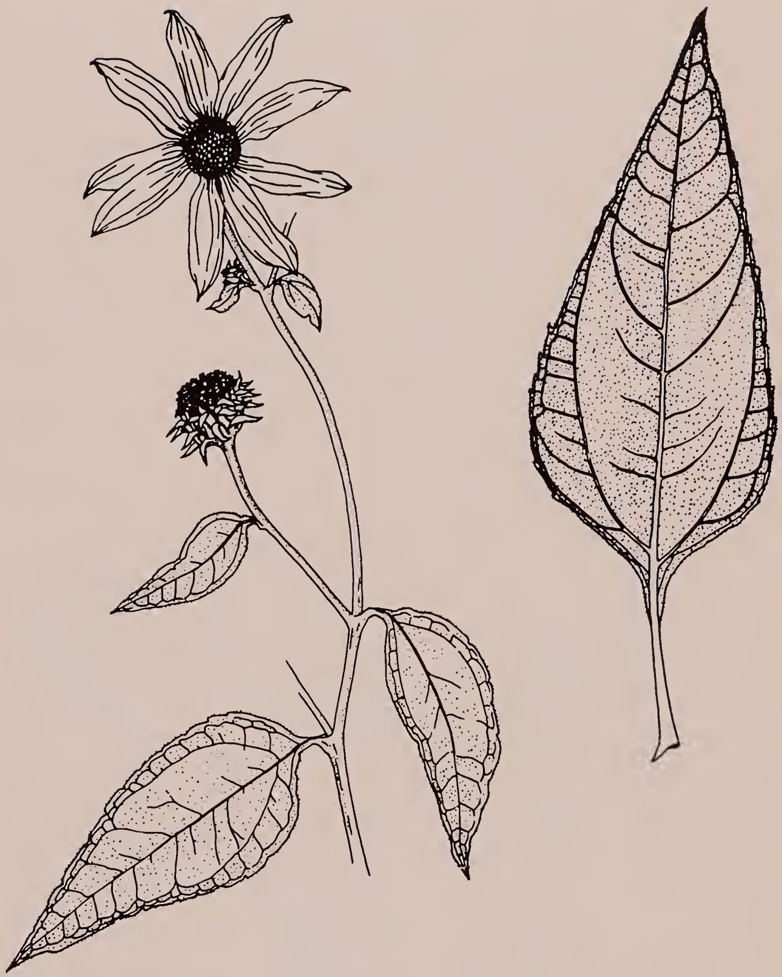


Fig. 27. *Helianthus strumosus*

H. strumosus var. *mollis* T. & G. Fl. N. Am. 2:327. 1842. (based on *H. mollis* Willd. Sp. Pl. ed. 4. 3:2240. 1800, not Lam.)

H. strumosus var. *macrophyllus* (Willd.) Britt. Mem. Torrey Club 5:335. 1894.

H. saxicola Small, Fl. S.E.U.S. 268. 1903. (T.: Georgia, Thomas Bold *Small* NY!)

H. australis Small, *l.c.* 1268. not Phil. 1845. (T.: Gerogia, Habersham Co., *Small* NY!)

H. strumosus var. *willdenowianus* Thell. Allgem. Bot. Zeitschr. 19:138. 1913.

H. strumosus var. *tomentulosus* House, Bull. N.Y. St. Mus. 254:726. 1924. (based on *H. mollis* Willd.)

H. montanus E. E. Wats. Pap. Mich. Acad. 9:403. 1929. (based on *H. australis* Small)

H. formosus E. E. Wats. *l.c.* 445. (T.: Missouri, Marion Co., *Davis 3274*, MO!)

H. leoninus E. E. Wats. *l.c.* 449. (Illinois: Lake Co., *Jensen*, MO!)

H. arenicola E. E. Wats. *l.c.* 453. (Illinois: Bureau Co., *Watson 767*, MSC!)

H. ambulans E. E. Wats. *l.c.* 456. (Indiana: St. Joseph Co., *Watson 170*, MSC!)

H. hirsutus var. *leoninus* (E. E. Wats.) Palmer & Steyermark, Ann. Mo. Bot. Gard. 22:672. 1935.

Rhizomes usually well developed, slender or stout, sometimes tuberous; stems 1.0-2.0 m. tall, stout or slender, glabrous and often glaucous, occasionally remotely setose, usually branched above; leaves all opposite or uppermost sometimes alternate, linear-lanceolate to broadly ovate, acuminate at tip, subcordate to cuneate at base, tapering to slender petiole 1.0-3.0 cm. long, margin entire, serrulate, or rarely deeply serrate, strumose-scabrous above, glaucous or green and glabrous to tomentulose beneath, triple veined, 7-18 cm. long, 2-10 cm. wide; heads few to many on short, stout, divergent or long, slender, ascending peduncles; disk 1.4-2.5 cm. in diam.; phyllaries lanceolate, acuminate or sometimes attenuate, erect, loose, or squarrose, equalling or exceeding disk, rarely leaf-like, glabrous to hispidulous on backs, usually ciliolate on margins, 2-4 mm. broad; rays 10-20, small to large (ca. 3.0 cm.); chaff 3-cuspidate to subentire, pubescent on tips and keel; achene 4.5-5.5 mm. long.

Chromosome number: n = 34, 51

Distribution: In deep woods or fully open habitats, roadsides and prairies throughout eastern North America from Quebec to Minnesota, south to northern Florida and northeastern Texas.

This "species," as treated here and quite evident from the description, is certainly the most variable among the perennials. Watson (1929) as can be seen in the number of his names in the list of synonyms, accepted several of the variants as species, but even if these are recognized, it still leaves *H. strumosus* as an extremely polymorphic species. It seems best at present to combine all of Watson's segregates with *H. strumosus.* Thus we are left with what may in a sense be described as a "wastebasket" species which serves to accommodate all the eastern polyploid sunflowers that cannot be placed in any other species. Although such "species" are a source or irritation to those who would like all species to be neat, orderly packages, it would be equally unsatisfactory to recognize numerous species which intergrade so extensively that it is impossible to put names on a large number of specimens. In fact, even the creation of varieties for some of the outstanding morphological variants hardly seems useful or likely to contribute to our understanding of the species.

Although we cannot offer any system of names adequate for this situation, we can, we feel, explain why this is and will likely continue to be the "rubbish heap" of the genus. The most likely origin of a majority of the tetraploid forms of this species is probably from hybrids of *H. divaricatus* x *H. grosseserratus* followed by chromosome doubling. This would result in a segmental allopolyploid which might be expected to show segregation. These tetraploids when crossed with various diploid species, the most likely candidates being *H. divaricatus, H. grosseserratus,* and *H. glaucophyllus,* would give triploids which when doubled would produce plants differing slightly from each other and their tetraploid progenitors but which would be able to exchange genes freely to produce a series of transitional types. Thus the first factor accounting for the great variability in this species stems from the fact that it has likely had origins from several different species and hybrids at different times and in different places.

A second important factor in the variability of this species and the impossibility of recognizing clear-cut regional variants stems from widespread hybridization involving a great number of species. The tetraploid form of the species has produced artificial hybrids in crosses with *H. decapetalus, H. hirsutus,* and *H. smithii.* At the hexaploid level artificial hybrids are known with *H. tuberosus, H. rigidus* and *H. resinosus.* It seems likely that such hybridization would not be uncommon in nature and that these hybrids and their derivatives would fall into *H. strumosus* as here delimited. Moreover, although we do not have the artificial hybrid between 4n and 6n forms of *H. strumosus,* the cross of *H. smithii* (4n) with *H. strumosus* (6n) was readily secured and showed high pollen stainability and some seed set. Thus, although we have not yet definitely identified such plants from nature, various pentaploids also may be included in *H. strumosus.*

A third factor is that since these plants are semi-weedy and frequently inhabit roadsides, it is likely that man has been responsible for their spread into many areas allowing for additional hybridization as well as the break down of any geographical races that may have developed. It is to be remembered that these plants reproduce both vegetatively by rhizomes as well as sexually.

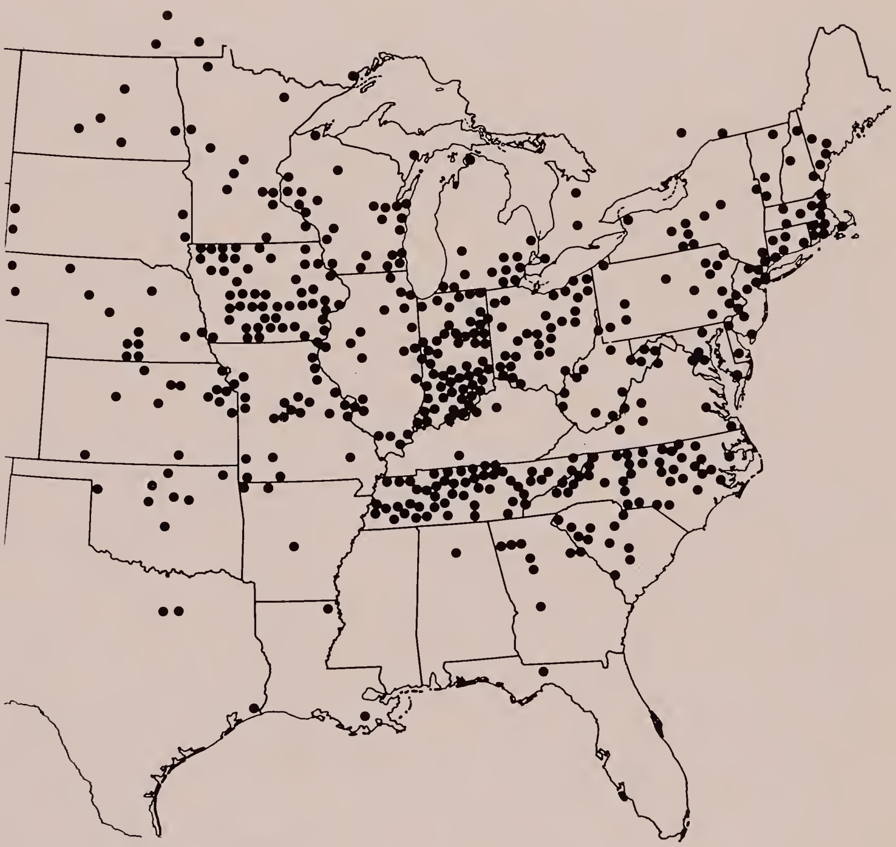
Watson's *H. leoninus* and *H. arenicola* are similar to the tetraploid forms of the species (*Heiser P7, P9, P73, P134, P137*) that have been grown at Bloomington. The general range of this part of the complex insofar as we can determine from field and herbarium studies extends from western Ohio to Nebraska, south to Oklahoma and probably also includes Watson's *H. vernalis*. The overall aspect of this phase is somewhat like *H. divaricatus* and *H. hirsutus*, differing from the former in its petiolate leaf and from the latter in its glabrous stem. However, stem pubescence is a variable character and in retrospect it appears that a more logical arrangement than the one adopted here would be to include the tetraploids of *H. strumosus* with *H. hirsutus*. However, since some tetraploids of *H. strumosus* are indistinguishable from certain hexaploids of the species which may occur within the same range, we have followed more or less the traditional treatment. Although pollen size of the hexaploids may be larger than those of tetraploids, there is an overlap of measurements, hence this character does not serve to separate tetraploids from hexaploids as well as it does to separate diploids from tetraploids.

Much of the eastern part of the range of *H. strumosus* is occupied by a robust glaucous-leaved hexaploid which in its extreme form is quite distinct, but to the west and south it grades imperceptibly into the pubescent-leaved forms. In the southern Appalachians the intergradation is with a very narrow leaved glaucous hexaploid, *H. montanus* of Watson.

Plants fitting the description of *Helianthus formosus* which Watson considered a well marked species are found in Illinois, Missouri, Arkansas and Oklahoma. These plants are characterized by a strongly glaucous lower leaf surface and produce small but well defined tubers. In the St. Louis area this form has always been found to occur with either *H. tuberosus* or *H. strumosus* but Jackson reports (oral communication) that some pure populations occur in Marion Co., Mo. Plants from both areas were hexaploid. Hybrids of "*H. formosus*" with *H. tuberosus* are fertile and give F_1 plants very similar to *H. tuberosus*. The exact disposition of these plants deserves additional study but they are placed with *H. strumosus* thus excluding glaucous leafed forms from *H. tuberosus*. The exact disposition of certain other names placed in synonymy is also somewhat problematical. *Helianthus macrophyllus* may be *H. tuberosus* or a hybrid. Gray (1884) considers Willdenow's *H. mollis* to be *H. strumosus* but Watson (1929) suspected that it might be *H. tuberosus.* One specimen from the New York Botanical Garden (no. 2, Carlyle, Ill.) labeled as *H. strumosus* var. *mollis* is actually *H. grosseserratus,* although Gray's description of his var. *mollis* seems to fall within the present concept of *H. strumosus.*

28. Helianthus tuberosus L. Sp. 905. 1753.

H. tomentosus Michx. Fl. Bor. Am. 2:141. 1803.
H. serotinus Tausch. Fl. 11:504. 1828.
H. esculentus Warcz. Allg. Gartenz. 20:293. 1852. (*fide* Watson, 1929)
H. vicetinus Turra ex. Zang., Atti Soc. Sci. Nat. Milan. 11:389. 1868. (*fide* Watson, 1929)
H. tuberosus var. *subcanescens* A. Gray, Syn. Fl. 12:280. 1884. (T.: Minn.? "Red River of the North," *Kennicot,* GH!)
H. subcanescens E. E. Wats. Pap. Mich. Acad. 9:430. 1929.



Map 28. *Helianthus tuberosus*

H. neomexicanus Woot. and Standl. Contr. U.S.N.H. 16:190. 1913. (T.: New Mexico, Grant Co., *Wooton* US!)

H. besseyi J. M. Bates, Am. Bot. 20:16. 1914. (T.: Nebr., Webster Co., *Bates 5816½*, NEB!)

H. tuberosus var. *typicus*. Ckll. Am. Nat. 53:188. 1919.

H. tuberosus var. *nebrascensis* Ckll. *l.c.* (T.: Cult. Colo. *Cockerell* US!)

H. tuberosus var. *alexandri* Ckll. *l.c.*

H. tuberosus var. *purpurellus* Ckll. *l.c.* 189.

H. tuberosus var. *fusiformis* Ckll. *l.c.*

H. tuberosus var. *albus*. Ckll. *l.c.*

H. tuberosus var. *purpurens* Ckll. *l.c.* 190.

H. tuberosus var. *multituberculatus* Ckll., Mon. Bull. Calif. St. Com. Hort. 8, no. 5: reprint p. 6. 1919.

H. nebrascensis Ckll. *l.c.* p. 7.

H. alexandri Ckll. *l.c.*

H. mollissimus E. E. Wats. Pap. Mich. Acad. 9:432. 1929. (T.: Missouri? *Glattfelter*, MO!)

H. tuberosus var. *tuberosus* Cronquist, Rhodora 47:399. 1945.

Rhizomes slender and usually terminally enlarged or tuberous; stems 1.0-2.8 m. tall, coarse, scabrous-hispid to somewhat hirsute, or rarely nearly glabrous, usually branched above; leaves opposite in lower third, alternate above, or all opposite or nearly so, ovate to oblong-lanceolate, scabrous above, whitish puberulent, hirsutulous or tomentulose below, usually coarsely serrate, 10-23 (-30) cm. long, 7-15 (-20) cm. wide, abruptly or gradually attenuate into winged or partially winged petioles, 2-8 cm. long; heads several to numerous; disks 1.0-2.5 cm. in diam.; phyllaries linear lanceolate to lanceolate, tips acute to short acuminate, equalling or slightly exceeding disks, 2-4 mm. wide, usually ciliate on margin and hispidulous on back, rarely nearly glabrous, frequently dark green and drying nearly black, loose and erect or sometimes reflexed at maturity; ray flowers 10-20, to nearly 4 cm. long and 1.2 cm. wide; pales 3-cuspidate, pubescent at summit; achenes glabrous, 5-7 mm. long.

Chromosome number: $n = 51$

Distribution: Damp or moderately dry, open or shaded areas, Nova Scotia to Manitoba, south to northern Florida and Texas. Widely cultivated and often escaping. Aug.-Oct.

As treated here this is an extremely variable species, although far less so than *H. strumosus*. One unifying feature is the possession of tubers, although these vary greatly in size, color, and shape. Tubers are sometimes reported as wanting under unfavorable conditions or in the southern part of its range

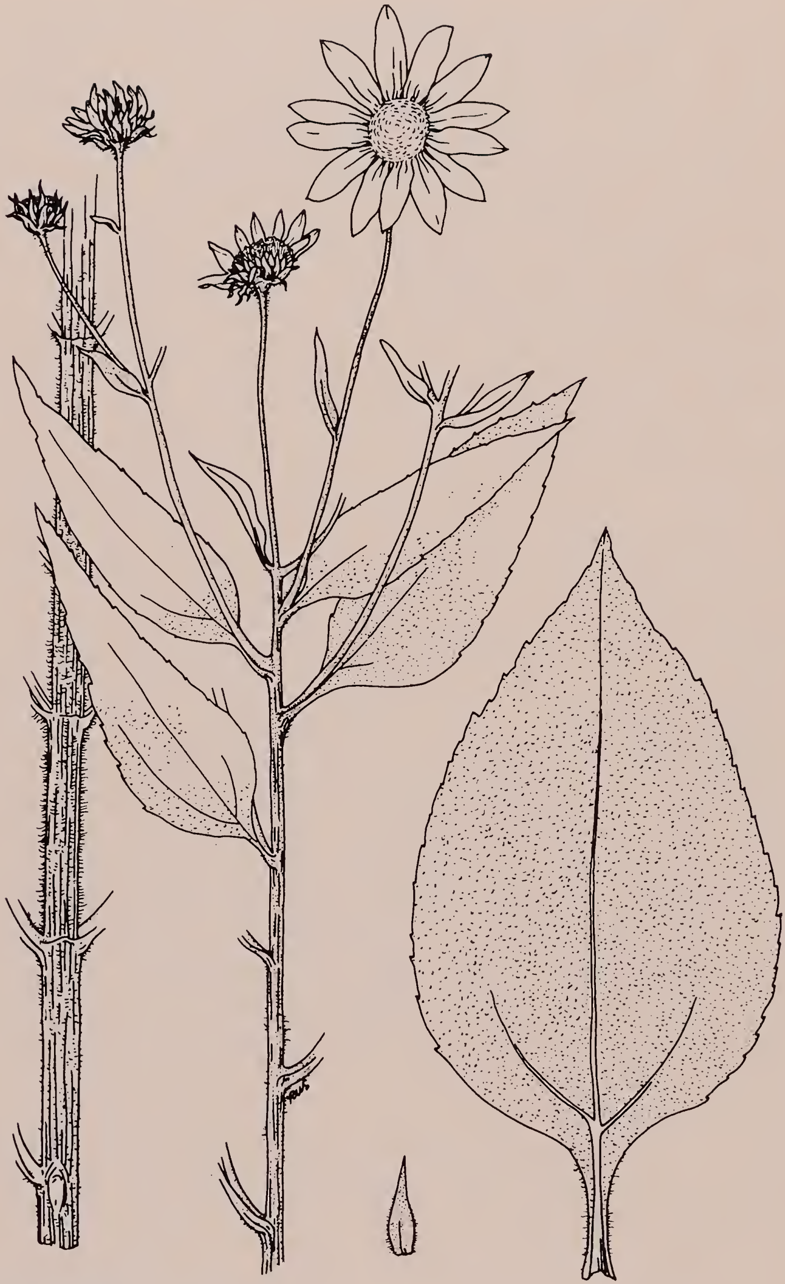


Fig. 28. *Helianthus tuberosus*

(Cronquist in Gleason, 1952). This may well be true but in some plants tubers are not produced until very late in the season. Small tubers may also be found in *H.* x *laetiflorus*, which is not unexpected if this is a hybrid with *H. tuberosus* as one of the parents. The only other species in which the rhizome may be decidedly thickened terminally and hence somewhat tuberous is *H. strumosus*, possibly resulting from hybridization with *H. tuberosus* although it could also be the result of the two species having very similar ancestors (see below). Unfortunately, underground parts are frequently not well represented on herbarium specimens, so the presence or absence of tubers is often of no value in identifying such material.

Even if tubers are not present, *H. tuberosus* is fairly readily separable from all other sunflowers except *H. strumosus.* Although the various extreme types of the two species are quite clear cut, the two species appear to grade into each other, which is not unexpected if the hypothesis that frequent hybridization occurs between the two is correct. In general, it may be stated that the stems of *H. tuberosus* tend to be more densely pubescent than those of *H. strumosus*, more of the leaves are alternate, the leaf is more coarsely serrate, broader and more strongly decurrent on the petiole and often more densely pubescent below, the phyllaries are often darker in color, and the rays may be somewhat longer. In spite of the apparent extensive intergradation between these two sunflowers, perhaps it is still wise to continue to recognize the two under separate species names.

At this time no satisfactory method of classifying all the variants within this species can be proposed. In recent floristic treatments the var. *subcanescens* is usually recognized. One of the principal characters of the variety, having most of the leaves opposite, seems to be strongly influenced by environmental conditions. Plants showing most of the upper leaves alternate, if left in the same spot in the garden for several years without cultivation, tend to produce shorter plants with nearly all opposite leaves. This, however, is not to deny that some of the variation in leaf arrangement is genetic, since some variation in this character has been observed in the some 25 collections of this species under cultivation at Bloomington.

Steyermark's (1963) concept of *H. tuberosus* var. *subcanescens* seems to be somewhat different from that of others. Material from Missouri annotated by him as such in the Chicago Natural History Museum probably would better be considered *H. strumosus.*

Several other names require brief mention. *Helianthus besseyi* represents a type of *H. tuberosus* occurring in the western part of the range of the species and is characterized by a somewhat thicker leaf. One might suggest introgression from *H. rigidus* to account for it.

Helianthus neomexicanus, although found outside of the "normal" range of *H. tuberosus*, appears to be a small but fairly typical member of that species. Since *H. tuberosus* is widely grown as a cultivated plant its occurrence in New Mexico is not surprising. Cockerell's numerous varieties are based primarily on tuber characteristics and serve to emphasize the great variation in the tubers. His observations were made on plants under cultivation at Boulder, Colorado. Watson's *H. mollissimus* which Fernald (1950) considers the same as var. *subcanescens* includes plants of *H. tuberosus* which are characterized by unusually heavy tomentum of the lower leaf surface. For a discussion of the European cultivated variants of this species, the reader is referred to Wagenitz's (unpubl.) forthcoming treatment.

Beatley (1963) has discussed the ecology of this species in some detail. Although it most frequently occurs in moist or poorly drained soils, it often thrives in dry soils in some areas. Her belief that this species had a wide, natural distribution may well be correct but certainly its distribution must have been increased after its adoption as a food plant by man. Although generally considered a cultivated plant of the North American Indian, the evidence for this is not too convincing (Heiser, upubl.). There is no doubt that it was a food widely used by the Indians, but whether the tubers were actually saved for planting or whether they were mainly gathered from wild sources is not always clear. It seems possible that *tuberosus* did not become a true cultivated plant until after its introduction into Europe. In any event, the accidental, if not intentional, spread of the plant by man must have occurred in prehistoric times; and in modern times, its distribution has certainly increased both intentionally as a cultivated plant and unintentionally as a weed.

Today, under the name topinambur or Jerusalem artichoke, both equally ridiculous but thoroughly delightful names, this species is a widely cultivated plant, although hardly a major one. The idea that the Jerusalem part of the name is a corruption of the Italian name for the sunflower, girasol, is still widely circulated but another more likely suggestion has been put forward by Salaman (1940) that it represents a corruption of Ter Neusen (Holland) from which place it was introduced into England. The recent breeding work being done on this species is summarized by Rudorf (1958).

The possible origin of this species has been discussed elsewhere (Heiser and Smith, 1964). Whether it is monophyletic or polyphyletic cannot be answered with certainty; either is possible. If the former is true, the present diversity in this species could have occurred partly by mutation and segregation (which might be expected in a segmental allopolyploid) and partly by hybridization with other hexaploids. If one examines living species and attempts to postulate possible progenitors, he might come up with either *H. decapetalus* or *H. hirsutus* as the tetraploid parent and several possible diploids, among which *H. giganteus* is a leading candidate. Because thus far it has been impossible to secure artificial crosses of diploid and tetraploid perennials, experimental proof of the origin is lacking. The possibility that the widely cultivated forms with their larger size might have a separate origin, for example from *H. hirsutus* x *H. annuus*, has been considered. This artificial hybrid, which is a triploid, has been produced and if doubled might be identified as *H. tuberosus*. However, if this were true, one might possibly expect some sterility in the cross of wild x cultivated *H. tuberosus* and this does not hold for the hybrids of this combination.

The origin of the tubers of this species has never been explained. They are not known to occur in diploid or tetraploid species but it should be pointed out that the rhizomes are slightly thickened at the tips in both *H. divaricatus* and *H. hirsutus* and that rather thick rhizomes are known for several diploid species. Thus the tubers might have originated in the hexaploid from the interaction of genes controlling rhizome development of the parental species. If *H. giganteus* or a tuberous rooted species is involved in the ancestry a second possibility is that the storage function of the root became transferred to the rhizome. The first hypothesis is probably more nearly correct.

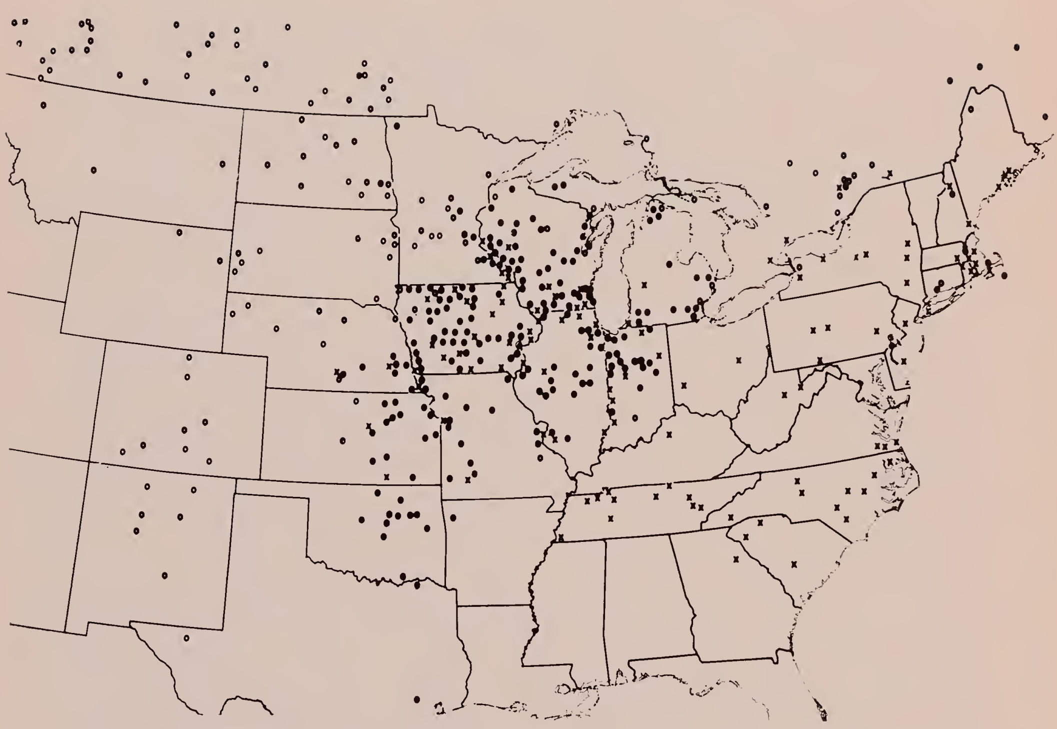
Artificial hybrids have been successful with all the hexaploids except *H. californicus* and *H. ciliaris*. Artificial hybrids have also been secured with one tetraploid, *H. hirsutus*; the hybrids produced some seeds and showed pollen stainability up to 40%. Artificial hybrids of this species with *annuus* are frequently mentioned in the European literature (e.g., Pustovoit, 1966). A detailed cytological study has recently appeared (Cauderon, 1965).

Natural hybridization of this species is known with *H. rigidus*, producing *H.* x *laetiflorus*. Artificial hybridization is also probably common with the hexaploid forms of *H. strumosus* (perhaps producing the plant called by Watson *H. formosus*), although detailed studies have not been made, and hybridization may occur with *H. resinosus*. In view of the comparative ease of securing artificial hybrids with the tetraploid *H. hirsutus* and the fact that the resulting pentaploid is vigorous and produces some seed indicate the possibility of natural hybrids with the tetraploids playing a role in the variation of this species, although *H. decapetalus* in many areas completes its flowering before *H. tuberosus* begins blooming. The artificial *tuberosus-hirsutus* hybrids are very similar to *H. tuberosus*, and it is quite likely that if such a hybrid appeared in herbarium material it would be labeled *H. tuberosus* without much hesitation.

29. Helianthus rigidus (Cass.) Desf. Cat. Pl. ed. 3:184. 1829.

Harpalium rigidum Cass. Soc. Philom. Paris. Bull. 141. 1818. (T.: Cultivated in Paris, P)

Viguiera rigida Hort., Gardn. Chron. n.s. 16:396. 1891.



Map 29. *Helianthus rigidus.* Solid dots, ssp. *rigidus*; open dots, ssp. *subrhomboideus*; X, *H. x laetiflorus*

Rhizomes stout, often terminally enlarged; stems 0.3-2.0 m. tall, sparingly to densely scabrous-hispid, green or more usually red, unbranched or sparingly branched above; leaves all opposite, or uppermost rarely alternate, linear-lanceolate to rhombic-ovate, serrate to subentire, gray-green to light green, rather thick, very scabrous, 5-21 cm. long, 2-6 cm. wide, decreasing in size up the stem and often becoming bract-like near heads, subsessile or with mostly winged petioles; heads generally 1-10 cm. on long, naked, or nearly naked, peduncles; disks 1.5-2.3 (-3.0) cm. in diam.; phyllaries elliptical to oblong-ovate, tip obtuse to acute, ciliate on margins, glabrous or sparingly hispid on backs, graduated, tightly appressed, usually dark green, shorter than disk, 3-5 mm. broad; rays deep yellow, 10-20, to 3.5 cm. long; disk flowers with reddish-purple lobes or yellow with reddish tips or rarely entirely yellow; pales entire or 3-cuspidate, somewhat pubescent on keel and tip; pappus usually with accessory scales; achenes 5-6 mm. long, glabrous or nearly so.

Chromosome number: n=51

The reddish disk flowers and the broad, short phyllaries readily serve to separate this species from all others except *H. atrorubens* and *H. silphioides.* The more highly reduced stem leaves of *H. atrorubens* and the distinctly petioled and broader leaves of *H. silphioides* readily separate these species from *H. rigidus.*

The variation of this species, complicated as it is by hybridization with *H. tuberosus,* makes the recognition of subspecific taxa difficult. Two major phases are evident, and in spite of extensive intergradation between the two there seems to be some merit in recognizing subspecific taxa as was done by Fernald (1946), who, however, did not recognize *H. laetiflorus* as a hybrid. That the two subspecies are more than ecological modifications is clear since they retain their differences when grown in the experimental garden.

In an earlier paper (Clevenger and Heiser, 1960) certain problems were raised in connection with the origin of these subspecies. *Helianthus rigidus* ssp. *subrhomboideus* and *H. tuberosus* represent the extreme types with *H. rigidus* ssp. *rigidus* and *H.* x *laetiflorus* being somewhat intermediate with the former approaching *H. rigidus* ssp. *subrhomboideus* and the latter approaching *H. tuberosus.* The interpretation that *H.* x *laetiflorus* represents a hybrid between *H. rigidus* ssp. *rigidus* and *H. tuberosus* is probably correct, but the origin of *H. rigidus* ssp. *rigidus* is more uncertain. Three possible explanations may be suggested (1) that *H. rigidus* ssp. *rigidus* is an established introgressant resulting from hybridization of *H. tuberosus* and *H. rigidus* ssp. *subrhomboideus*; (2) that *H. rigidus* ssp. *rigidus* and *H. rigidus* ssp. *subrhomboideus* arose from one original type and have gradually differentiated into two subspecies or (3) that the two have separate origins from the hybridization of, for example, the same tetraploid with different diploid species which, followed by chromosome doubling, gave rise to the two subspecies.

Although the third hypothesis is in some ways the most appealing, we are at a loss to supply the names of the species involved in the origin of *H. rigidus.* In spite of the ease of hybridization with the other hexaploids, *H. rigidus* is extremely different from them and may come from entirely different progenitors. The nature of the phyllaries in *H. rigidus* is particularly difficult to explain since somewhat similar phyllaries are confined to the series Atrorubentes and Ciliares whose species for the most part do not overlap the present-day natural distribution of *H. rigidus*; *Helianthus silphioides,* however, does reach Arkansas and Illinois. The only tetraploid that could conceivably be involved in the origin is *H. hirsutus* whose distribution overlaps that of both *rigidus* and *silphioides.* Another diploid that may possibly be involved in some way is *H. occidentalis.* We, of course, have no way of knowing what morphological features might result from the interaction of these genomes but one would hardly think that the phyllary character of the diploid (*H. silphioides*?) would dominate that of the tetraploid

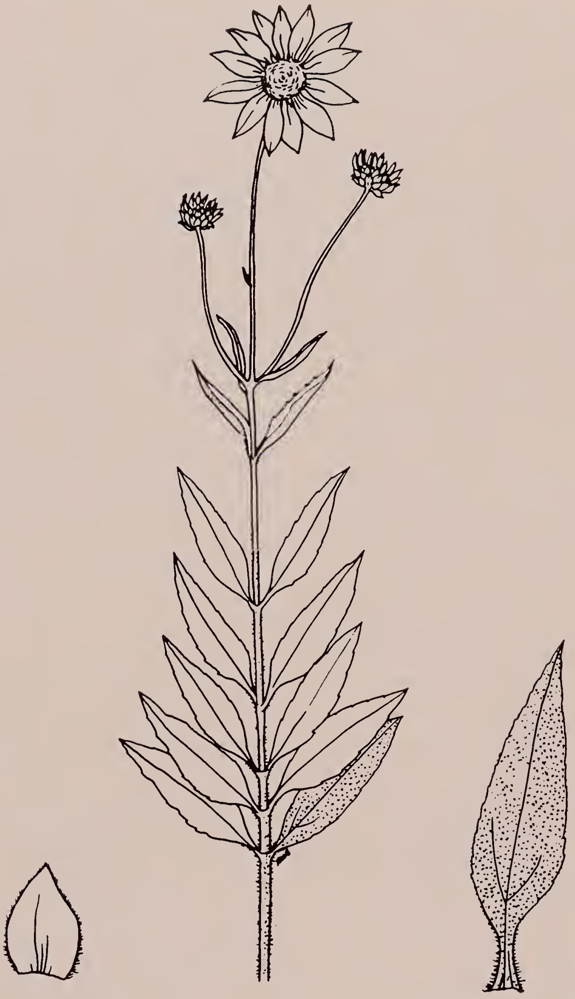


Fig. 29. *Helianthus rigidus*

parent (*H. hirsutus*?). However, neither of these species overlaps the distribution of ssp. *subrhomboideus* so we would have to assume, based on evidence of present distributions, that ssp. *rigidus* in a western migration gave rise to ssp. *subrhomboideus.* One way out of the dilemma, of course, is to assume that the origin of these subspecies took place at a time when the distribution of the various species was somewhat different from that of today or that species, now extinct, were involved in the origin or origins of these subspecies.

It should also be pointed out that ssp. *subrhomboideus* is rather similar to some individuals of *H. nuttallii* ssp. *rydbergii*; moreover its distribution is almost entirely within the area occupied by *H. nuttallii.* Fernald (1946) is inclined to think that the eastern migration of ssp. *subrhomboideus* is by way of transcontinental railways, although there is no strong reason for not considering it prehuman. The distribution of ssp. *rigidus,* on the other hand, most nearly parallels that of *H. grosseserratus.*

The synonymy of this species is rather involved and it is difficult to determine precisely to which subspecies a given name should be referred. The oldest name widely used for this species is *H. laetiflorus*; but since it seems fairly certain that the type is a hybrid between *H. rigidus* and *H. tuberosus* (Heiser, 1960a; Clevenger and Heiser, 1963), the name *rigidus* must be employed for this species. Cassini's description of an erect, branching plant about five feet high, as well as the likelihood that it was from an eastern source, is the basis for associating this name with the more eastern subspecies. The name *H. diffusus* is a source of confusion since the illustration depicts a plant with brown disk (from plants grown in England from seeds collected in Missouri by Nuttall) which is probably ssp. *rigidus* whereas the description states that the species has a yellow disk. Nuttall's *H. parviflorus* from "lower Louisiana" is difficult to identify precisely but his later comparison (1841) of it with *H. crassifolius* would suggest *H. rigidus* ssp. *rigidus.* Two of Elliott's names pose even greater problems from the standpoint of their geographical source since they come from the "western districts of Georgia." His *H. scaberrimus* may be *H.* x *laetiflorus.* Since this species was early in cultivation in Europe, perhaps it had already been introduced into Georgia and escaped. Torrey and Gray (1843) "confidently refer *H. tricuspis*" to *H. laetiflorus* "although the specimens in the herbarium are exceedingly imperfect," and it probably belongs with *H.* x *laetiflorus*; the description also somewhat suggests *H. hirsutus.* Torrey and Gray's (1843) variety *beta* of *H. rigidus,* excluding the synonymy, fits fairly well ssp. *subrhomboideus* as here treated. Deam's *H. rigidus* f. *flavus* appears to be a fairly typical *H. rigidus* ssp. *rigidus* except for the yellow disk flowers. Several horticultural varieties of *H. rigidus* were named by Dewar (1893), most of which are probably referable to ssp. *rigidus.*

Artificial hybrids of the two subspecies of *H. rigidus* are fertile and artificial interspecific hybrids of both subspecies have been secured with *H. strumosus* and *H. tuberosus.*

Key to Subspecies

Plants usually 1-2 m. tall; leaves usually oblong-lanceolate to lance-ovate, 8-27 cm. long, acuminate . . . . *H. rigidus* ssp. *rigidus*

Plants usually 1.2 m. or less tall; leaves rhombic-ovate to linear-lanceolate, 5-12 cm. long, acute or obtuse . . . . *H. rigidus* ssp. *subrhomboideus*

29a Helianthus rigidus ssp. rigidus

H. diffusus Sims, Curtis' Bot. Mag. 46:2020. 1818.

H. pauciflorus Nutt. Gen. Am. 2:177. 1818.

H. missuricus Spreng. Nov. Prov. Hart. 21. 1819.

H. crassifolius Nutt. Trans. Amer. Phil. Soc. N.S. 7:367. 1841. (T.: Plain of the Arkansa, *Nuttall,* BM; Photo, GH!)

H. missouriensis Schwein. ex. Nutt. *l.c.* 368.

H. diffusus var. *missouriensis* Appelton, Garden 34:430. 1888.

H. rigidus f. *flavus* Deam, Fl. Ind. 975. 1940. (T.: Ind., Newton Co., *Deam 57312,* IND!)

H. laetiflorus var. *rigidus* Fern. Rhodora 48:79. 1946.

Plants erect; leaves few to several, all opposite or uppermost alternate, usually 7 or more pairs, subsessile or with petioles to 2 cm. long; peduncles frequently with bracts or reduced leaves; heads generally several; lobes of disk-corollas deep red to almost entirely yellow; phyllaries oblong-ovate, to 12 mm. long.

Distribution: Dry to moderately wet prairies, Wisconsin to southern Manitoba, south to eastern Texas; occasional as weed or escape from cultivation more eastward. Aug.-Sept.

29b Helianthus rigidus ssp. subrhomboideus (Rydb.) *stat. nov.*

H. subrhomboideus Rydb. Mem. N.Y. Bot. Gard. 1:419. 1900. (T.: Nebr., Grant Co., *Rydberg 1627,* NY!)

H. scaberrimus var. *subrhomboideus* Farwell, Amer. Midl. Nat. 8:278. 1923.

H. laetiflorus var. *subrhomboideus* Fern. Rhodora 48:79. 1946.

Plants erect or ascending; leaves few, all opposite, 5-7 (-9) pairs, sessile or with petioles to 1.0 cm.; peduncles usually with few or no bracts; heads mostly 1-5; phyllaries elliptical to oblong-ovate, to 10 mm. long; corollas of disk-flowers deep red or red-purple.

Distribution: Dry, open places; southern Ontario to southern Alberta, south to western Texas; occasionally more eastward as a weed. 500 to 7800 feet. July-Aug.

29c Helianthus x laetiflorus Pers. (*H. rigidus* x *tuberosus*)

H. laetiflorus Pers. Syn. Pl. 2:476. 1807. (T.: P, photo IND!)
H. tricuspis Ell. Sketch. 2:422. 1824.
H. scaberrimus Ell. *l.c.* 423. 1824.
H. laetiflorus var. *tricuspis* T. & G. Fl. N. Am. 2:323. 1843.
H. severus. E. E. Wats. Pap. Mich. Acad. 9:428. 1929. (T.: Kansas, Pottawatomi Co., *Watson 744* MSC!)
H. superbus E. E. Wats. *l.c.* 461. (T.: Cult. Mass., *Watson 363*, MSC!)

This is one of the two hybrids in the genus that appears deserving of a distinct name, primarily because it is widely cultivated as an ornamental. The name is being supplied for F_1 hybrids and hybrid derivatives that are more or less intermediate between *H. rigidus* and *H. tuberosus*. Such individuals are distinguished from *H. rigidus* most readily by their yellow disk-flowers and more acute phyllaries, and from *H. tuberosus* by their shorter phyllaries and more scabrous leaves. Obviously backcrossing produces individuals showing various degrees of intermediacy so that it becomes quite arbitrary as to where the line is drawn. Since this sunflower has been in cultivation for nearly 200 years and there has been some selection of ornamental types, some horticultural forms have longer and more numerous ray flowers than are found in either putative parent.

The status of *H. laetiflorus* as a good species was discussed in 1877 (N.H.P. in Bot. Gaz. 2:144) but its probable hybrid origin was not yet suspected. The reasons for considering it a hybrid are presented by Clevenger and Heiser (1963). Inspection of the map reveals, however, that this taxon is rather frequent in some areas where neither of its parents occurs, and these are most probably escapes from cultivation. Beatley (1963), because of its frequency in certain areas of Tennessee, suspects it of being native there. Although we are fairly confident of its hybrid origin, it is, of course, not impossible for a sunflower having the same or nearly the same characteristics as this hybrid to have originated in a manner similar to that of the other hexaploids.

In an earlier paper (Heiser 1960a) it was pointed out that often ornamental or escaped plants of *H. laetiflorus* are barren of seed, probably as the result of a single clone being established. Since that time we have learned that some plants which we identified as *H.* x *laetiflorus* and which show high pollen stainability produce only small amounts of seeds when pollinated with other plants of *H.* x *laetiflorus* or with the putative parents. Most F_1 artificial hybrids of *H. tuberosus* x *rigidus* show high to moderate seed set. Thus, it seems possible that the nearly sterile type may be later hybrid derivatives rather than F_1's.

Two of Watson's species are placed in synonymy here. His *H. severus*, while somewhat different from most plants of *H.* x *laetiflorus*, is rather similar to some of the artificial hybrids of *H. rigidus* ssp. *subrhomboideus* x *H. tuberosus*. His *H. superbus* closely resembles *H. tuberosus*, particularly in its phyllaries, but shows other features of *H.* x *laetiflorus* and possibly is a backcross. Its burial here is perhaps as logical as under *H. tuberosus*. (See also discussion of synonymy under *H. rigidus*).

Series 2. Gigantei

Roots usually becoming enlarged, often tuber-like and fascicled; rhizomes usually short (less than 15 cm. long) and rather thick; stem leaves well developed, mostly alternate, usually numerous, usually lanceolate and 1-nerved, rarely linear or ovate; disks small to large; lobes of disk-corolla yellow except in *H. salicifolius*; achenes 4-5 mm. long. (Gray in 1884 resorted to geography in his key to species and unfortunately it is still necessary to do so.)

Key to Species of Series Gigantei

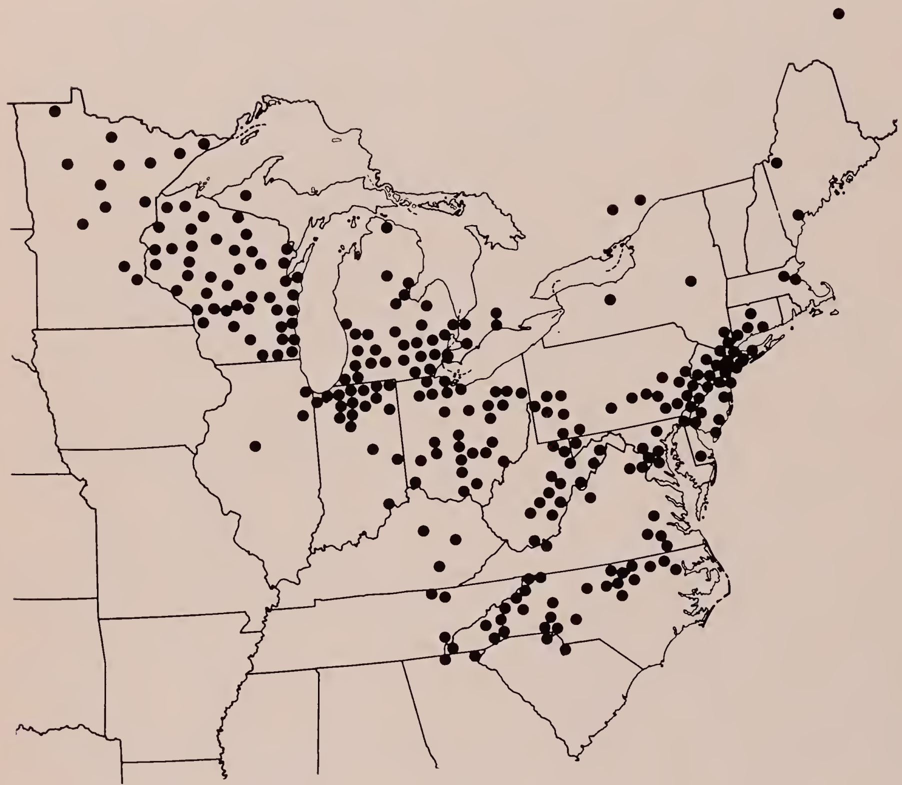
Disk-flowers with red or purple lobes; leaves linear-lanceolate..............34. *H. salicifolius*

Disk flowers with yellow lobes; leaves lanceolate to ovate.

- Leaves usually conduplicate and entire or nearly so; inflorescence frequently spiciform; phyllaries long attenuate..............................33. *H. maximiliani*
- Leaves not conduplicate, entire or serrate; inflorescence usually paniculate; phyllaries rarely long attenuate.
  - Heads less than 1.6 cm. in diam; phyllaries shorter than disks; leaves rather densely pubescent on both surfaces, usually revolute.............37. *H. schweinitzii*
  - Heads usually over 1.6 cm. in diam; phyllaries usually equalling disk or longer; leaves usually not densely pubescent above, not revolute.
    - Leaves subsessile or with short ciliate petioles; stems hispid to hirsute; leaves scabrous or somewhat hirsute below; phyllaries usually ciliate; eastern North America...................................30. *H. giganteus*
    - Leaves subsessile (rarely) to fairly long petiolate, petiole usually not ciliate; stems glabrous to hispid or tomentose; phyllaries glabrous or short ciliate to densely pubescent.
      - Phyllaries usually 3 mm. or more broad near base, reflexed at maturity.
        - Stems glabrous, Calif. to Baja Calif................35. *H. californicus*
        - Stems usually hispid to hirsute, southeastern United States ....36. *H. resinosus*
      - Phyllaries less than 3 mm. broad, not reflexed, nearly glabrous to tomentose.
        - Stems generally glabrous; leaves mostly alternate, tomentulose to hispid below, dark shiny green and nearly glabrous above; central and eastern United States.................31. *H. grosseserratus*

Stems usually pubescent; leaves mostly alternate to mostly or all opposite, hispid below and light green and nearly glabrous above, or somewhat tomentose on both surfaces; Canada and western United States........................32. *H. nuttallii*

30. Helianthus giganteus L. Sp. Pl. 905. 1753. (Photo, GH!)



Map 30. *Helianthus giganteus*

H. altissimus L. Sp. Pl. ed. 2, 1278. 1763. (T.: LH, Photo in Watson, Pap. Mich Acad. 9: Pl. LXX. 1929.)
H. virgatus Lam. Encyc. 3:85. 1789.
H. altissimus var. *virgatus* Pers. Syn. 2:476. 1807.
H. gigas Mich. Fl. Bor. Am. 2:141. 1803.
H. giganteus var. *subtuberosus* Britton, Ill. Fl. N. St. and Can. 3:425. 1898. (T.: see discussion)
H. subtuberosus Britton, Man, Fl. N. States and Can. 993. 1901.
H. giganteus var. *altissimus* Farwell, Rept. Mich. Acad. Sci. 17:180. 1916.
H. giganteus var. *virgatus* Farwell, *l.c.*

H. giganteus var. *oppositifolius* Farwell, *l.c.* (T.: Mich. St. Clair Co. *Farwell 3884*, BLH!)

H. giganteus var. *resiniferus* Farwell, Amer. Midl. Nat. 10:218. 1927. (T.: Mich. Oakland Co. *Farwell 3846*, BLH!)

H. giganteus var. *verticillatus* Farwell, *l.c.* (T.: Mich. Oakland Co., *Farwell 4369* BLH!)

H. giganteus var. *microcephalus* Peattie, Am. Midl. Nat. 10:131. 1926. (T.: Ind., Lake Co., *Umbech*, Sept. 9, 1897. Stated to be at US but not found)

H. validus E. E. Wats. Pap. Mich. Acad. 9:410. (T.: North Carolina, *Harbinson* in 1897, GH!)

H. borealis E. E. Wats., *l.c.* 411. (T.: Minn. Ramsey Co., *Aiton*, MIN!)

H. membranaceus *l.c.* 438. 1929. (T.: Minn. Ramsey Co., *Sandberg*, Aug. 1891. MIN!)

H. alienus E. E. Wats. Pap. Mich. Acad. 9:406. 1929. (T.: North Carolina: Buncombe Co. *Biltmore Herbarium 2482a.* MO!)

H. giganteus ssp. *alienus* Long, Rhodora 56:201. 1954.

H. exasperatus E. E. Wats. Pap. Mich. Acad. 9:455. 1929. (T.: Wisc., Brown Co. *Schuette* in 1886, WIS!)

H. giganteus var. *subtuberosus* f. *verticillatus* Lakela, Rhodora 49:21. 1947. (T.: Minn., St. Louis Co., *Lakela 6140* MIN!)

H. subtuberosus f. *verticillatus* Boivin, Nat. Canad. 87:36. 1960.

Roots thickened, tuber-like, sometimes fleshy, usually becoming woody; stem 1.0-4.0 m. high, usually stout, hispid, scabrous or hirsute, usually reddish; leaves mostly alternate, rarely all opposite, blades lanceolate-ovate to lanceolate, shallowly serrate to subentire, scabrous or strumose above, sparingly hirsute below, 8.0-20.0 cm. long, 1.4-3.5 cm wide, subsessile or with ciliate petioles to 1.2 cm. long; disks 1.8-2.4 cm. in diam.; phyllaries linear-lanceolate, equalling or exceeding disk in length, 1.5-2.0 mm. wide, loose, usually conspicuously ciliate on margins, surface short-pubescent to subglabrous; rays 12-20, pale yellow, 1.5-2.5 cm. long; disk corollas usually pubescent near base; chaff shallowly tricuspidate to nearly entire, middle cusp acute, pubescent; achene glabrous, 3-4 mm. long.

Chromosome number: n = 17

Distribution: Common in wet and occasional in moderately dry, usually open places from Nova Scotia to Minnesota, south to northern Georgia and west to Illinois. Aug.-Oct.

Helianthus giganteus is a rather variable species, certainly in a large part the result of hybridization with other species as well as the usual environmental modification found in sunflowers. The nearly sessile leaf and the

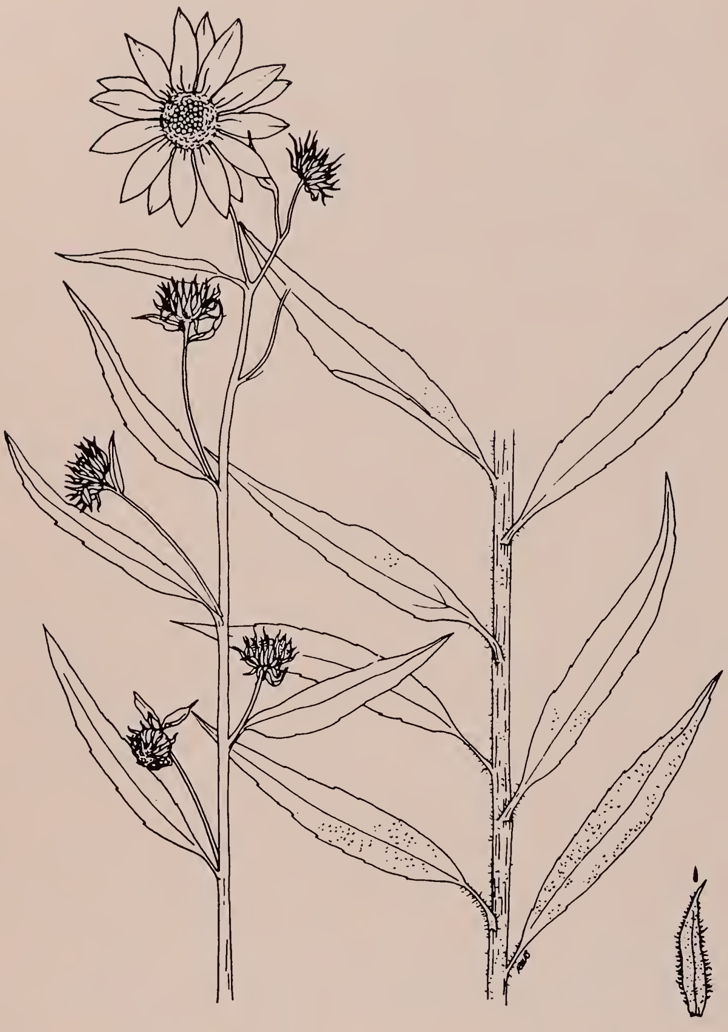


Fig. 30. *Helianthus giganteus*

hairy stem and its occurrence in rather wet areas are perhaps some of the most reliable characters distinguishing this species. Its closest relatives are *H. grosseserratus* and *H. nuttallii*.

The interaction of *H. giganteus* with *H. grosseserratus* is now fairly well understood (Long 1960, 1961) and far greater problems are posed by the nature of the populations that occur in the northern part of the range where it seemingly grades into *H. nuttallii*. The treatment of the specimens from this area is far from adequate and detailed field studies are needed. The identification of the specimens was made some years ago and a restudy would probably result in some change. The map which more or less shows the species stopping at the northern border of the United States is hardly realistic. Throughout most of its area, except for obviously depauperate individuals, *H. giganteus* has most of the leaves alternate but in the northern part of the range the leaves are often mostly or all opposite. Whether this results from hybridization with *H. nuttallii* or whether it is a clinal type of variation cannot be answered adequately at present.

Long (1961) has considered that *H. giganteus* was centered in Appalachia during the Pleistocene. It is of some interest that the populations which Watson called *H. alienus* are more or less concentrated in this area. It is possible that these represent populations nearest the original type (it should also be pointed out that this is also the area where *H. giganteus* is uncontaminated by hybridization with *H. grosseserratus*). If *H. giganteus* were originally centered in Appalachia and moved northward with the retreat of the glaciers and in time encountered *H. nuttallii* with subsequent hybridization, the present variation pattern could have resulted.

On the other hand, it should be pointed out that the age of this species is unknown. Less likely than the above hypothesis, but worthy of consideration, is the possibility that *H. giganteus* is a recent immigrant into Appalachia having moved down from the northern states and in response to local conditions it gradually changed from an *H. nuttallii* type of plant into *H. giganteus*, which would make the "alienus" types the most recent rather than the most ancient element of the species. Whatever may be the real situation, the fact remains that *H. giganteus* is at the most a border-line species.

Long (1961) has discussed the synonymy and I agree with him on most names. The type of Watson's *H. membranaceus* is probably referable to *H. giganteus* rather than a hybrid. Long considers it a hybrid of *H. giganteus* and *H. grosseserratus*. In some ways it appears nearer to *H. decapetalus* than it does to *H. grosseserratus*. It is uncertain as to what Watson's *H. validus* is, but Long's disposition of it here is as logical as any place. Watson's *H. exasperatus* appears to be a fairly typical *H. giganteus*.

The name *H. subtuberosus* has long been a source of confusion. Recently Boivin (Nat. Canad. 87:36. 1960) has treated it as a species but he apparently was not aware of Watson's conclusions on the subject. The name comes from a Bourgeau specimen in the Hooker Herbarium. Gray in 1884 treated it as a synonym of *H. giganteus.* Britton in 1901 was the first to adopt the name and cites Gray but unfortunately did not give a type. Watson (1929) examined what he considered was "Bourgeau's original specimen" and concluded that it was "perfectly typical *H. maximiliani*" and designated a new name, *H. borealis,* for what he thought represented the current concept of "*H. giganteus* var. *subtuberosus.*" The type could be a somewhat atypical specimen of *H. giganteus.* Long (1961) has concluded that it is a hybrid or hybrid derivative of *H. giganteus* x *H. grosseserratus.* There are two Bourgeau specimens at the herbarium of New York Botanical Garden. His number *31* from "sources of the St. Croix River" is probably an atypical *H. giganteus* and the second labeled "Fort Ellice, 1831" may well be the specimen on which Britton based his concept. To complicate matters still further Lakela has named a form "*verticillatus*" of var. *subtuberosus,* although there was already a form *verticillatus* of *H. giganteus* itself. Boivin then transferred Lakela's form to the species *H. subtuberosus,* and, although by the Code this form would be typified by Lakela's specimen, he has designated a new type (Canada: Sask. *Melford, Boivin* and *Mosquin 11462A,* DAO) which may well fit into *H. nuttallii* as interpreted here. Finally, Long (1966) has described a subspecies *canadensis* of *H. nuttallii* (which is here placed in synonymy with *H. nuttallii* ssp. *nuttallii*) for the plant which "frequently passes under the name *H. subtuberosus* Britton." Thus there are several choices open as to names for "*giganteus* var. *subtuberosus*" if one is needed. It is perhaps unwise, however, to use any name until additional field study can be undertaken. There exists, however, particularly in Minnesota and perhaps elsewhere in the northcentral United States and across southcentral and southeastern Canada plants which do not quite fit into either *H. nuttallii* or *H. giganteus;* and it would certainly be desirable to have more information concerning them, even though a detailed study of them may not lead to any reasonable taxonomic solution.

In addition to natural hybrids with *H. grosseserratus* (x *H. luxurians*) and the probable occurrence of hybrids with *H. nuttallii,* natural hybrids are known with several other species. Hybrids with *H. divaricatus* are known and could well be responsible for some of the occurrence of opposite leaves in *H. giganteus.* Putative hybrids with *H. maximiliani* are found in Wisconsin and Minnesota. The hybrid with *H. mollis* apparently explains the origin of the long puzzling *H. doronicoides* (Jackson, 1956); although the type apparently comes from a garden in Europe, putative natural hybrids are also known. A few specimens have also been seen which suggest hybrids with *H. microcephalus* and *H. occidentalis.*

Artificial hybrids, mostly showing high pollen stainability and regular meiosis, have been secured with *H. atrorubens*, *H. decapetalus* (2n), *H. divaricatus*, *H. grosseserratus*, *H. maximiliani*, *H. mollis*, *H. nuttallii*, and *H. salicifolius*.

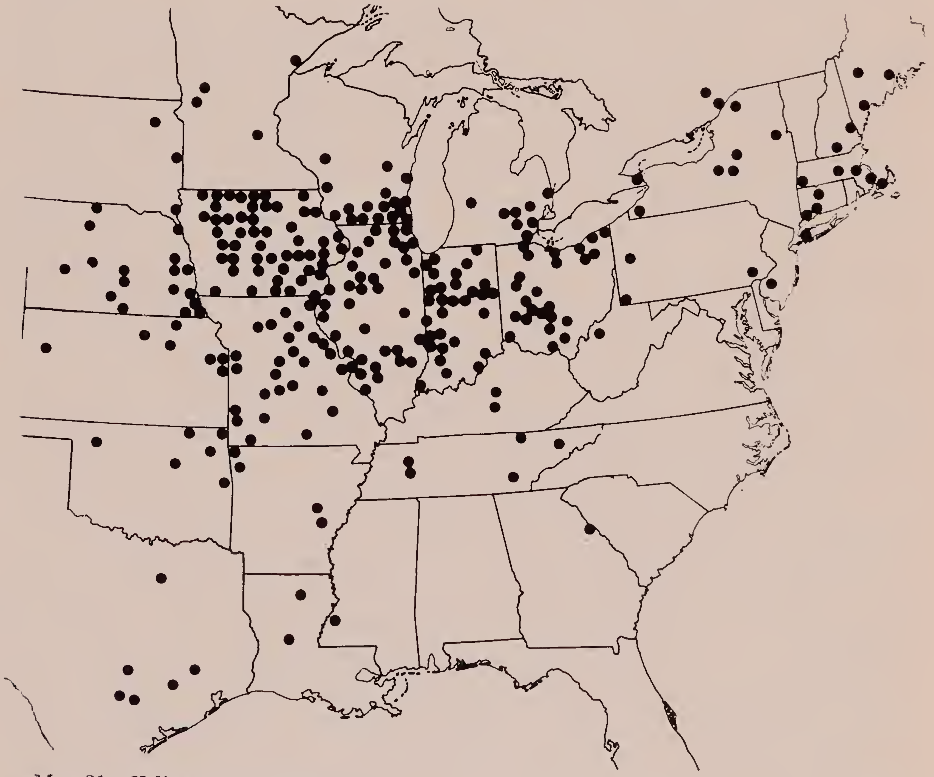
31. Helianthus grosseserratus Martens Sel. Hort. Lov. 1839. ex Linnaea 14, Litt. p. 133. 1840. (Type locality: St. Louis, Mo. Neotype: Mo., Jasper Co., *E. J. Palmer 1343* MO., dupl. at IND)

H. grosseserratus var. *hypoleucus* A. Gray: Syn. Fl. 1²:276. 1884. (T.: Texas, *Drummond*, GH!)

H. instabilis E. E. Wats. Pap. Mich. Acad. 9:423. 1929. (T.: Ill., Clark Co., *Watson 147* MSC!)

H. grosseserratus f. *plenifolius* Wadmond, Rhodora 34:19. 1932. (T.: southeastern Wisconsin, *S. C. Wadmond* GH).

H. grosseserratus ssp. *maximus* Long, Rhodora 56:199. 1954. (T.: Nebr., Richardson Co., *H. C. Reynolds* 2643, NEB!)



Map 31. *Helianthus grosseserratus*

Rhizomes short to medium long; roots thickened, becoming woody; stem 1.0-5.0 m. high, stout, usually glabrous and glaucous below, glabrous to scabrous or sparingly appressed pubescent above; leaves lanceolate to lanceolate-ovate, 20.0-32.0 cm. long, 1.5-9.0 cm. wide, mostly alternate, coarsely to shallowly serrate, rarely subentire, scabrous above, rarely canescent, usually densely puberulent to short tomentose beneath, tapering to petiole, 2.0-5.5 cm. long; heads usually numerous, 1.5-2.5 cm. in diam.; phyllaries linear-lanceolate, about 1.5 mm. wide, slightly exceeding disk, loose, glabrous or ciliate on margins, glabrous or rarely tomentulose on backs, rays 14-20, 2.5-4.0 cm. long, bright yellow; lobes of disk-corollas sparingly pubescent to nearly glabrous at base; chaff entire or shallowly 3-cuspidate, middle cusp acuminate, densely short pubescent; achene glabrous, 3-4 mm. long.

Chromosome number: $n = 17$

Distribution: In dry or moderately wet prairies or other open places, New England to South Dakota, south to Texas. Late August-Oct.

Among the diploid sunflowers, *H. giganteus, H. grosseserratus*, and *H. nuttallii* and its subspecies pose some of the most difficult problems from the standpoint of classification. A strong case might be made for considering them members of a single highly variable species, but some system of distinguishing them by means of names seems desirable. One might, of course, recognize them as varieties or subspecies. One of the reasons for maintaining them as species is tradition. All taxonomists, including rather conservative ones, such as A. Gray, M. L. Fernald, and Cronquist, have maintained most of these taxa as species. Although it must be admitted that tradition should not guide scientific judgment, I have decided to maintain them as species and to try to point out their nature as clearly as possible, since no appreciable increase in knowledge results from a change in their status.

Actually, in spite of extensive hybridization, *H. grosseserratus* maintains itself as a very distinct entity over most of its range. The glabrous or nearly glabrous stem, the flat, lanceolate, usually distinctly serrate, fairly long petioled leaves, usually distinctly serrate, and tomentose or tomentulose on the lower surface in combination serve to distinguish it from species with which it is sympatric.

As Long (1961) has shown, hybridization of *H. grosseserratus* is common with *H. giganteus* where their ranges overlap and introgression has apparently resulted in the creation of aggressive weedy races in both species. It may be that we are witnessing the amalgamation of two partially formed species. But at the present the amalgamation has not proceeded far enough to prevent assigning the vast majority of individuals to one species or another.

Much more difficult to explain, stemming in part from the lack of any detailed studies, is the situation in the western part of the range of the species.

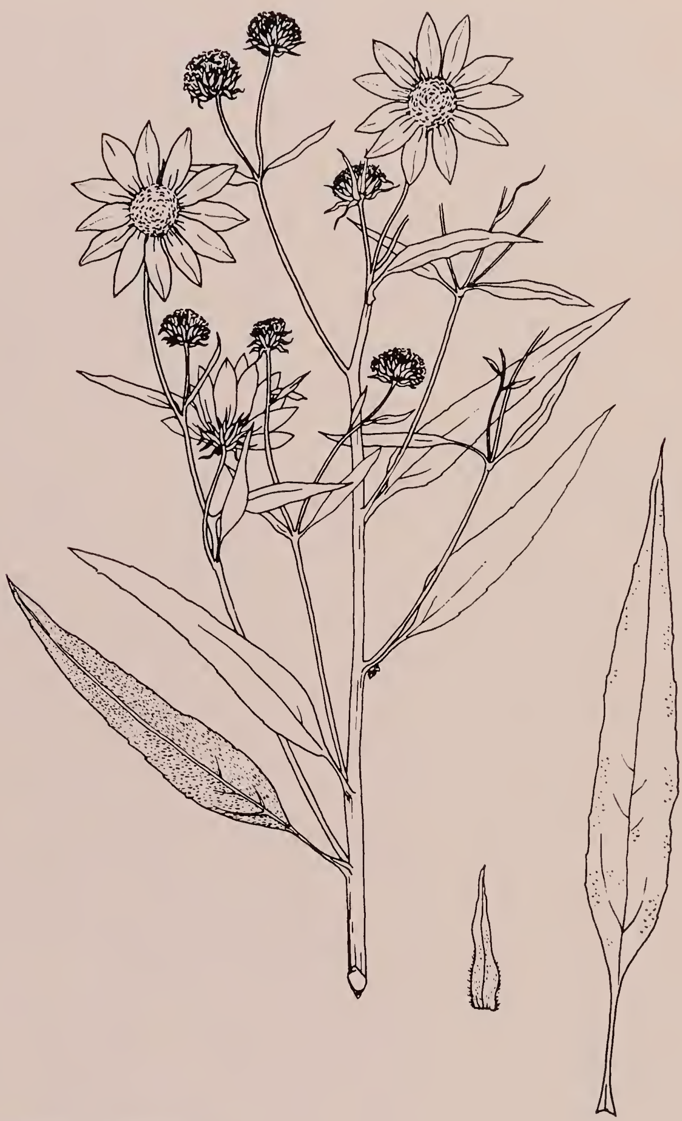


Fig. 31. *Helianthus grosseserratus*

In this area the usually reliable tomentose pubescence of the lower leaf surface is replaced by a scabrous type of pubescence and in Nebraska and South Dakota this species grades into the nebulous taxon, *H. nuttallii* ssp. *rydbergii*. In this area those individuals with lanceolate leaves have been somewhat arbitrarily assigned to *H. grosseserratus* and those with more ovate types of leaves to ssp. *rydbergii* which, while hardly a satisfactory solution, is all that can be accomplished until field studies are undertaken. Equally puzzling is the occurrence of *H. grosseserratus*-type individuals within the range of *H. nuttallii* (see discussion under that species).

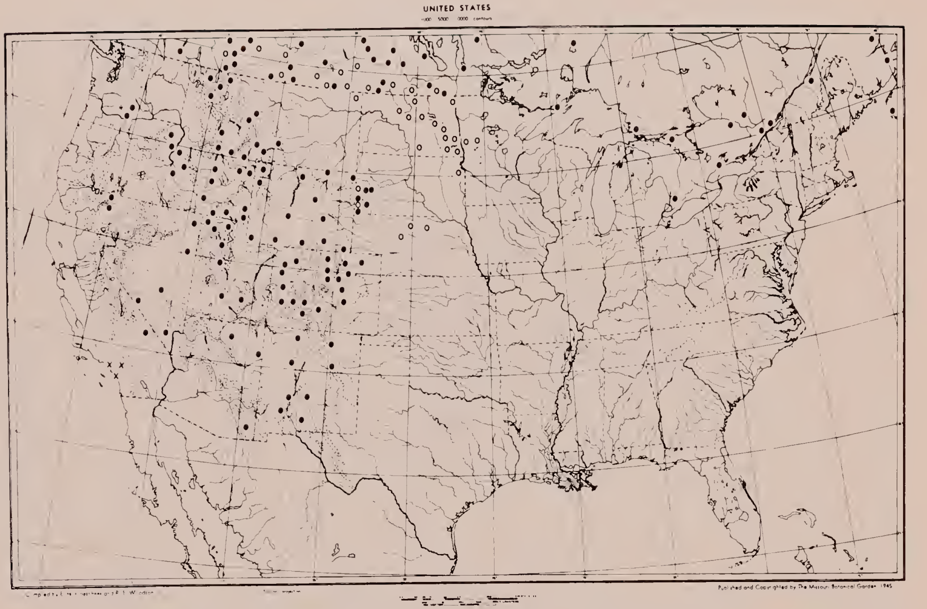
In addition to the hybrids with *H. giganteus*, and the probability of hybridization with *H. nuttallii* ssp. *rydbergii*, natural hybrids are known with *divaricatus, maximiliani, mollis, occidentalis*, and *salicifolius*. Arkman and Thorne (1956) have reported hybrids with *H. tuberosus*; the specimen on which this report was based was not included in the material sent from Iowa. Since these two species occur together in many places and their blooming dates may overlap slightly there is certainly opportunity for hybridization. However, ten years of attempts to produce this hybrid artifically using different strains of both species have been unsuccessful. Artificial hybrids, however, have been secured with several diploid species: *atrorubens, divaricatus, giganteus, maximiliani, mollis, nuttallii, occidentalis, salicifolius.*

The area occupied by this species today was for the most part glaciated. Whether the species persisted during glacial times to the south (Texas?) and spread northward with the retreat of the glaciers or whether its origin is entirely in post-glacial times is not known. It appears to be spreading today as a roadside weed and it seems likely that its occurrence in New England has come about in the last hundred years.

Long (1961) has discussed the synonymy of this species. Little needs to be added. Long's subspecies *maximus* differs from what he considers to be the typical element by a single character, the deeply serrate leaf, and occurs with the typical element. Hence, it would appear more nearly to be a *forma.* Moreover, although the type apparently is no longer in existence, the name chosen for the species by Martens and his description suggests that the typical element is the same as Long's subspecies. Long (1961) considers *H. instabilis* to refer to hybrids or hybrid derivatives of *H. grosseserratus* and *H. giganteus.* While I would agree that Watson's concept of this species included such hybrids, the type itself appears to belong to *H. grosseserratus* and was collected in an area where *H. giganteus* is unknown.

32. Helianthus nuttallii T. & G. Fl. N. Am. 2:324. 1842. (T.: Plains of Lewis River, *Nuttall* PH!)

Roots thick, often tuber-like and fascicled, rhizomes usually short; stems 0.5-4.0 m. tall; stems glabrous to slightly hispid, occasionally glaucous or



Map 32. *Helianthus nuttallii.* Solid dots, ssp. *nuttallii*; open dots, ssp. *rydbergii*; X, ssp. *parishii*

somewhat hirsute; leaf arrangement quite variable, from mostly alternate to all opposite, narrowly lanceolate to nearly ovate, entire or serrate, 4-20 cm. long, 1.0-4.0 cm. wide, nearly glabrous to hispid or rarely densely tomentose above, hispidulous, rough hispid to villous or tomentose below, subsessile to short petiolate; disk 1.0-2.0 cm. in diam; phyllaries usually linear-lanceolate, equalling or slightly exceeding disk in length, appressed pubescent, rarely nearly glabrous, to tomentose, rarely short ciliate on margin, 1.5-2.0 mm. wide.

An extremely variable and poorly understood species. The treatment which follows is hardly adequate and perhaps partly artificial but seems to be the best solution at the present time.

Key to Subspecies

Phyllaries sparingly pubescent to glabrous, leaves hispid to hispidulous below

Leaves mostly alternate, narrowly to broadly lanceolate, acute to acuminate, to 20 cm. in length; plants generally 2.0-3.0 m. tall; mostly Rocky Mountains and Canada . . . . *H. nuttallii* ssp. *nuttallii*

Leaves mostly or all opposite, lanceolate to nearly ovate, acute to obtuse, to 15 cm. in length; plants generally 1.0-2.5 m. tall; northern Great Plains . . *H. nuttallii* ssp. *rydbergii*

Phyllaries usually densely pubescent, leaves tomentulose to villous-tomentose below, southern Calif. . . . . *H. nuttallii* ssp. *parishii*

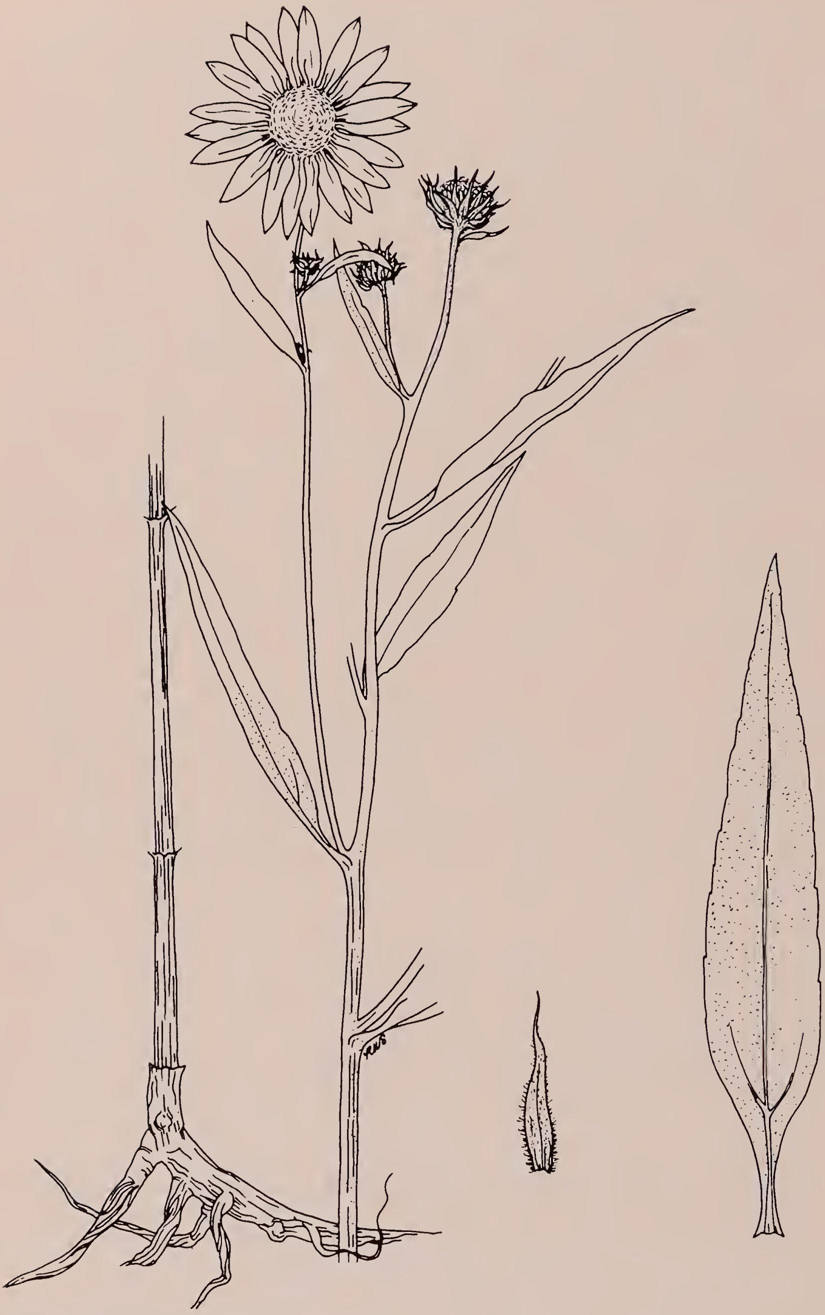


Fig. 32. *Helianthus nuttallii*

32a Helianthus nuttallii ssp. nuttallii

H. giganteus var. *utahensis* D. C. Eaton. Bot. King's Expd. 169. 1871. (T.: Utah: Wahsatch Mts., *S. Watson 603* US!)

H. californicus var. *utahensis* A. Gray, Syn. Fl. N. Am. 12:227. 1884.

H. utahensis A. Nels. Bull. Torrey Club 29:405. 1902.

H. fascicularis Greene, Pl. Bak. no. 3. 28. 1901. (T.: Colorado: Montrose Co., *Greene*, ND!)

H. coloradensis Ckll. Proc. Biol. Soc. Wash. 27:6. 1914. (T.: Colorado: Boulder Co., *Cockerell*, US!)

H. coloradensis var. *andrewsi* Ckll., *l.c.* p. 7. (T.: Colorado: Boulder Co., *D. M. Andrews*, unknown)

H. coloradensis f. *suphurea* Ckll. Torreya 18:181. 1918. (T.: Colorado: Boulder Co., *Andrews*, unknown)

H. parishii var. *coloradensis* Ckll. Torreya, *l.c.*

H. bracteatus E. E. Wats. Pap. Mich. Acad. 9:393. 1921. (T.: Utah: Cache Co., *Mulford 177* MO!)

H. nuttallii ssp. *coloradensis* Long, Rhodora 56:199. 1954.

H. nuttallii ssp. *canadensis* Long, Brittonia 18:77. 1966. (T.: Canada, Manitoba: Dist. de Souris, *Boivin* and *Alex 10245*, DAO, isotype, IND!)

Plants (1.0-) 2.0-3.0 m. tall; stem usually glabrous, sometimes glaucous, or hispid to scabrous; leaves 10-20 cm. long, narrowly to broadly lanceolate, mostly alternate but sometimes all but uppermost opposite, moderately to densely hispid below, generally short petiolate; heads few to numerous, 1.5-2.0 cm. in diam., phyllaries nearly glabrous to appressed pubescent.

Chromosome number: n = 17

Distribution: generally in moist places, across southern Canada to Nebraska and south in mountains to New Mexico and Arizona.

If certain Canadian plants of this taxon are compared with individuals from the southern Rockies, it would hardly appear that they could belong to the same subspecies, but there is such complete intergradation that it has not been possible to reach a more satisfactory treatment. Specimens from Colorado and New Mexico are remarkably similar to *H. grosseserratus*, but as interpreted here the two species are completely allopatric. In general, *H. nuttallii* ssp. *nuttallii* can be distinguished from *H. grosseserratus* by less glaucous stems, a greater number of opposite leaves, entire or less conspicuously serrate leaves which also are usually somewhat smaller and lighter in color, a rough leaf undersurface in contrast to the softer one of *H. grosseserratus*, and a shorter petiole.

In the Dakotas and southcentral Canada ssp. *nuttallii* grades into ssp. *rydbergii* and in turn the material about the Great Lakes and eastern Canada becomes difficult to distinguish from *H. giganteus.* Whether to refer *H. subtuberosus* to this complex or to *H. giganteus,* as has been done here, poses a problem. Long (1966) has created the subspecies *canadensis* for some of this material, and this name may serve for those who feel a name is necessary for this material, much of which has passed as "*H. subtuberosus*" in herbaria. However, it is hardly equivalent to the other subspecies recognized in this revision. The overall distribution of ssp. *nuttallii* as recognized here is not too dissimilar to that of *H. rigidus* ssp. *subrhomboideus* (see discussion under that species). The Canadian material which Long (1961, fig. 5; *Turner 2128, Breitung 7138*) has treated as *H.* x *luxurians,* occurs at some distance from the nearest known source of *H. grosseserratus,* one of its putative parents, and should probably be referred to ssp. *nuttallii* or perhaps to hybrids of ssp. *nuttallii* and *H. giganteus.*

The variation in ssp. *nuttallii* has resulted in a long list of synonyms. The only one requiring discussion is Watson's *H. bracteatus* which is distinguished by long filiform bracts on the peduncle. In other characters it appears to fall well within the confines of ssp. *nuttallii.* Thus far it is known only from the type specimen.

H. nuttallii ssp. *nuttallii* is sympatric with *H. pumilus* in parts of the western United States. I have never seen the two growing together but it is possible that they do so. One specimen which has been placed with ssp. *nuttallii,* (Colo: near Denver, *Eastwood 89*) in its pubescence, blunt leaves, and broad obtuse phyllaries approaches *H. pumilus.* However, attempts at securing artificial hybrids between the two taxa have been unsuccessful.

Plants of *H. nuttallii* have been grown in the field at Bloomington for several years. They are, however, much smaller than those in nature, and tend to die back in the hot weather of late July and August, although by this time some seed has usually matured. Artificial hybrids have been produced with *H. giganteus* and *H. grosseserratus* which give over 90% pollen stainabilities and hybrids with *H. maxmiliani* showed 70% stainable pollen. Two weak hybrids have also been secured with *H. niveus* which gave pollen counts of 10%.

32b Helianthus nuttallii ssp. parishii (A. Gray) Heiser, Contr. Dudley Herb. 4:316. 1955.

H. parishii A. Gray, Proc. Amer. Acad. 14:7. 1883. (T.: Calif., San Bernardino Co., *Parish 1025* GH!)

H. californicus var. *parishii* Jepson, Man. Fl. Pl. Calif. 1077. 1925.

H. oliveri A. Gray, Proc. Amer. Acad. 20:299. 1885. (T.: Calif. Los Angeles Co., *Oliver* GH!)

H. parishii f. *oliveri* Ckll. Torreya 18:181. 1918.

Stems 2.0-4.0 m. tall, glabrous to tomentose; leaves mostly alternate, 10-20 cm. long, 1.5-2.5 cm. wide, lanceolate, hispid to densely tomentose above, tomentulose to tomentose or somewhat villous below, shallowly serrate to entire, subsessile to short petiolate; peduncles tomentulose or tomentose; heads rather numerous; disks 1.5-2.0 cm. in diam.; phyllaries tomentulose to tomentose.

Chromosome number: unknown

Distribution: in swampy or other wet places, southern California, to 1500 feet. Aug.-Oct.

In the present context it would perhaps be equally logical to treat this taxon as a species. It is the only member of this assemblage that apparently does not hybridize with other taxa and hence does not show intergradation, since it is geographically isolated from related taxa. Thus it is a geographical race, and this, combined with its very minor differences from southern populations of *H. nuttallii*, perhaps justifies treatment as a taxonomic subspecies.

It is also rather similar to *H. californicus* (see under that species) and *H. grosseserratus*. A densely pubescent form of *H. grosseserratus* (Gray's var. *hypoleucus*) is also known and, of course, it is most likely that this represents a parallel development rather than indicating common origin.

Helianthus nuttallii ssp. *parishii* represents the farthest extension of the diploid members of section Divaricati into the southwest. Whether this results from a western migration of its progenitor or whether it originally evolved here and gave rise to the other members of the group through an eastern migration is not known. Elsewhere it has been suggested that the genus is probably southwestern in origin so the latter possibility is of some interest.

This subspecies now appears to be very rare and may be on the verge of extinction, apparently because of the destruction of its habitat by man. The densely pubescent form (*H. oliveri*) has not been collected since the 1920's and recent collections of the typical element are few.

32c Helianthus nuttallii ssp. rydbergii (Britton) Long, Brittonia 18:77. 1966.

H. rydbergii Britton, Man. Fl. N. States and Can. 993. 1901. (T.: Hooker Co., Nebr., *Rydberg 1767* NY!)

H. nitidus Lunell, Amer. Midl. Nat. 1:236. 1910. (T.: North Dakota, Butte. *Lunell 1150*, MIN!)

H. nitidus var. *camporum* Lunell, *l.c.* p. 237. (T.: North Dakota, Leeds. *Lunell 383*, MIN!)

H. apricus Lunell, *l.c.* (T.: North Dakota, Leeds. Sept. 10, 1900. *Lunell*, MIN!)

H. apricus var. *camporum* Lunell, Amer. Midl. Nat. 2:127. 1911.

H. nitidus var. *trifoliatus* Lunell, Amer. Midl. Nat. 5:64. 1917. (North Dakota, Butte, *Lunell 1152*, MIN!)

H. subtuberosus var. *rydbergii* Boivin, Nat. Canad. 87:36. 1960.

Stems 0.7-2.0 m. tall, usually scabrous or somewhat hispid, sometimes nearly glabrous; leaves all opposite, to mostly alternate, 3.5-12 cm. long, 2-5 cm. wide, ovate-lanceolate to nearly ovate, scabrous above, hispid to scabrous below, rather pale green and thick, subentire to serrulate to shallowly serrate, short petiolate; peduncles scabrous, heads usually few, disks 1.0-1.8 cm. in diam., phyllaries usually finely ciliate on margins, subglabrous to somewhat pilose on backs.

Chromosome number: n = 17

Distribution: southern Manitoba to Alberta south to Nebraska. Sandy, dry soils to wet places. Aug.-Sept.

Watson (1929) remarked that *H. rydbergii* "is not one of the more characteristic or strongly marked species," certainly an understatement. His claim that it was "abundantly distinct" is hardly true, although the name serves the purpose of being a convenient depository for a number of specimens that cannot be placed in either the typical element of *H. nuttallii* or with *H. grosseserratus*. As Watson correctly pointed out, it is "extremely variable."

In Nebraska and perhaps in Minnesota it seemingly passes into *H. grosseserratus* and in the western part of the Dakotas and in Canada it intergrades with *H. nuttallii* ssp. *nuttallii*, and some plants suggest an influence of *H. maximiliani*. However, in parts of North Dakota and Canada there is a fairly distinctive element, rather short plants with small mostly opposite, nearly ovate leaves, suggesting somewhat both *H. pumilus* and *H. rigidus* var. *subrhomboideus*. If it were not for the large number of intermediates with *H. nuttallii* ssp. *nuttallii* and *H. grosseserratus*, one might be justified in giving specific rank to these populations. Study of the map reveals somewhat of a discontinuity in the range, with specimens from South Dakota being rare. Whether this approaches the true distribution or whether it is simply the result of the lack of collecting in South Dakota is not known. Data on the habitat seem somewhat conflicting since it is recorded from extremely wet places as well as from dry places. The variability suggests that we may be dealing with more than one "element" or perhaps with no element at all but a series of hybrids involving various species. However, it is difficult to explain the small ovate type of leaf on the basis of the latter hypothesis.

Since the taxon is a diploid, the explanation used for the complex situation in *H. strumosus* does not hold and it seems possible that detailed studies of populations might give a better understanding of the variation and perhaps result in a more realistic taxonomic disposition than the one employed here, which admittedly is not satisfactory.

For hybridization attempts involving this subspecies, the reader is referred to Long (1966).

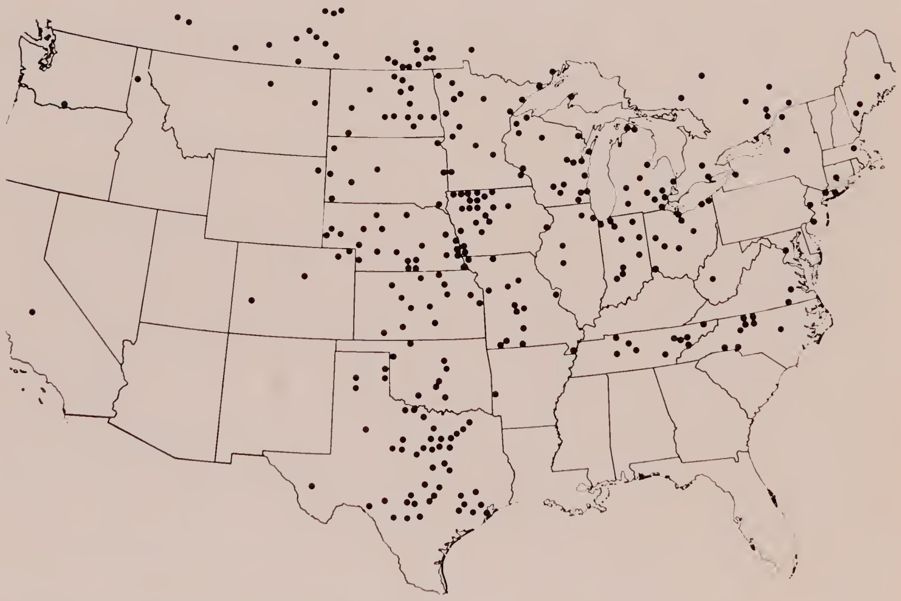
33. Helianthus maximiliani Schrader, Ind. Sem. Hort. Götting. 1835. (Neotype: Mo., Ray Co., *Steyermark 72797*, MO)

H. maximiliani var. *asperrimus* Engelm. and Gray, Boston Jour. Nat. Hist. 5:249. 1845. (T.: Texas, "between the Brazos and the Colorado" *Lindheimer 261*, MO!)

H. maximiliani var. *iubaris* Lunell, Amer. Midl. Nat. 5:63. 1917. (T.: North Dakota, Leeds. *Lunell 1147*, MIN!)

H. maximiliani var. *paniculata* Farwell, Pap. Mich. Acad. Sci. 3:107. 1924. (T.: Michigan, Monroe Co., *Farwell 6290* BLH!)

H. maximiliani f. *pallidus* Clute, Am. Bot. 36:17. 1930. (T.: North Dakota, Grand Forks, *Clute*, stated to be at Butler but not located there.)



Map 33. *Helianthus maximiliani*

H. dalyi Britton, Jour. N.Y. Bot. Gard. 2:84. 1901. (T.: Long Island Sag Harbor, *Britton*, NY!)
H. maximiliani var. *dayli* Farwell, Rep. Mich. Acad. Sci. 17:180. 1916.
H. attenuatus E. E. Wats. Pap. Mich. Acad. 9:416. 1929. (T.: "cult. ex sem N. Mex., Memphis" *A. Fendler*, MO!)

Rhizomes well developed, stems usually several, light green or sometimes light red, 0.5-3.0 m. tall, scabrous to scabrous-hispidulous, frequently densely so near summit; leaves rather numerous, mostly alternate, lanceolate, 10-30 cm. long, 2.0-5.5 cm. wide, usually somewhat falcate and conduplicate, light green to gray-green, upper and lower surfaces scabrous to scabrous-hispidulous, margins usually entire, rarely obscurely serrate, sessile or with petioles to 2 cm. long; heads few to many, when numerous usually in spiciform or racemose arrangement; disks 1.6-2.8 cm. in diam.; phyllaries linear-lanceolate and usually long attenuate, conspicuously exceeding disk, loose, white canescent on backs, ciliate on margins, 1.5-2.5 mm. wide; rays large (usually 2.5-3.5 cm. long), sometimes concave; chaff linear acuminate, entire or obscurely 3-cuspidate, pubescent at tip; achenes 3-4 mm. long.

Chromosome number: n = 17

Distribution: dry to moderately wet ground, prairies, plains, and waste ground, across southern Canada to North Carolina west to the Rockies, with greatest concentration from Manitoba to Texas. July (in northern part of range) to Sept.-Oct. (in southern part of range).

This is a fairly well marked species throughout most of its range but, as is true for most sunflowers, the important diagnostic characters of the leaves are so modified in depauperate individuals that identification becomes uncertain. The characteristics of the leaf—usually light green or gray-green, entire, sessile or short petiolate, and conduplicate and the whitish canescent—and the rather long attenuate phyllaries are usually quite diagnostic. In well-developed individuals the somewhat spike-like arrangement of the heads is also fairly unique. This species is one of the most showy in the genus and has long been appreciated as a garden ornamental.

As can be seen from the map, *H. maximiliani* has a wide distribution (in addition to those localities shown it is also known from Kootenani Co., Idaho, and Fresno Co., Calif.). It is difficult to determine its pre-white man area but it may have been limited to the plains and prairies of the central and western region. How much of the area occupied elsewhere due to accidental spread from wild plants or escapes from cultivation is difficult to determine—probably both have been involved.

Its closest relationships appear to be with *H. grosseserratus* and *H. nuttallii*. Long (1959) has made detailed studies of the natural hybrids with *H. grosse-*

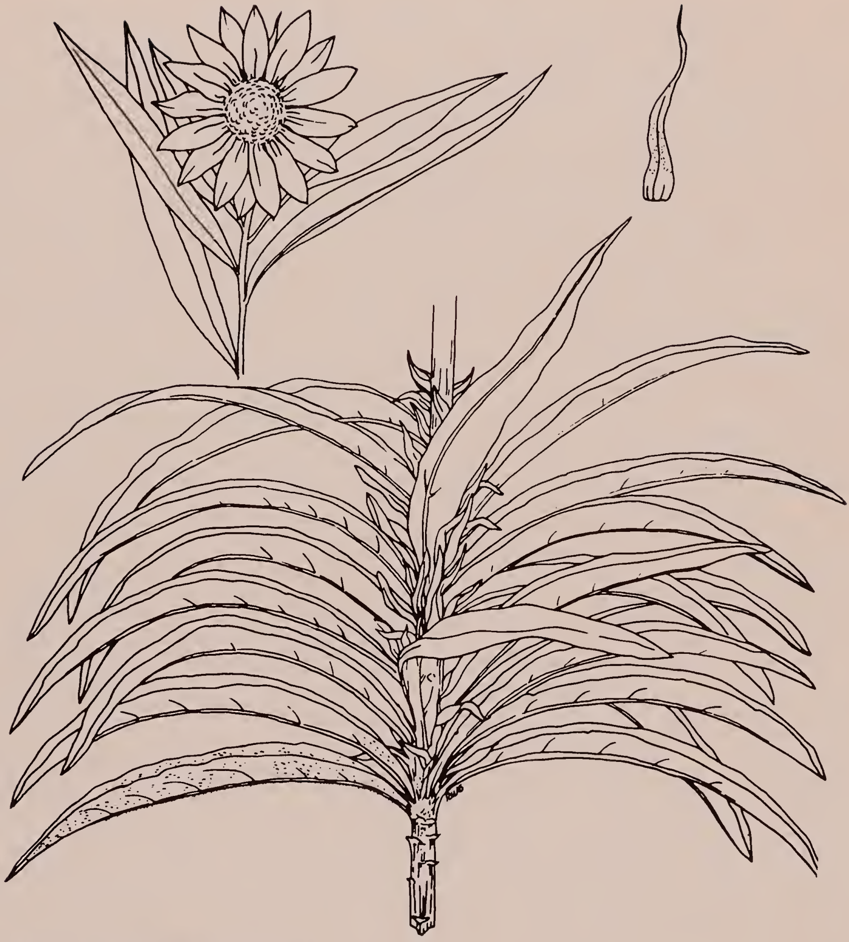


Fig. 33. *Helianthus maximiliani*

serratus, and apparently little back crossing results in nature, although artificial backcrosses are readily secured. Putative natural hybrids are also known with *H. giganteus* and *H. salicifolius*, and the possibility that hybridization has occurred with *H. angustifolius* is discussed under *H. simulans*. The hybridization of *H. maximiliani* with *H. nuttallii* in Canada seems likely and deserves investigation. However, on the whole, for a perennial sunflower, hybrids in this species are relatively rare, which probably contributes to its being one of the better "species" of this group. Artificial hybrids, however, have quite readily been secured with a number of species— *H. angustifolius*, *decapetalus* (2n), *giganteus*, *grosseserratus*, *longifolius*, *mollis*, *occidentalis*, *nuttallii*, and *salicifolius*.

Detailed studies might show the existence of north-south clines in the species for some characters. Plants from Canada in the experimental garden at Bloomington are 0.7-1.0 m. tall, with relatively small heads and leaves, and come into bloom in late June; whereas plants from Texas reach heights of nearly 3 meters, have relatively large heads and leaves, and do not start flowering until late September.

Watson (1929) states that the type of this species is probably in the herbarium of the University of Göttingen, Germany. Dr. R. Borkamm of that institution informed me (litt., 1959) that there was no type of this species there; therefore, it is necessary to designate a neotype.

Helianthus dalyi of Britton is apparently simply a depauperate form of this species. The *H. attenuatus* of Watson is somewhat more difficult to interpret. It was grown in 1852 from seeds supposedly collected in "New Mexico;" the state of New Mexico today is outside of the known range of this species. However, the type specimen appears to be fairly typical of *H. maximiliani* except for the phyllaries which are somewhat longer than is ordinarily seen in this species. The varieties and the form listed in synonymy are simply minor variants hardly worthy of taxonomic recognition.

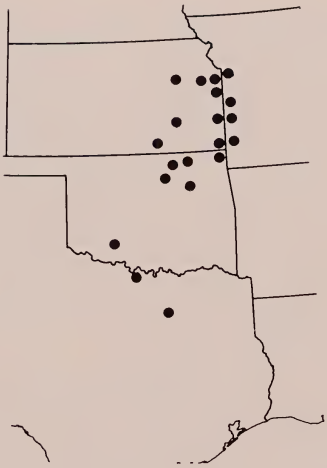
34. Helianthus salicifolius A. Dietr., Otto and Dietr. Allg. Gartenz., 2:337. 1834. (T.: *Collector unknown*, s.n. B, *fide* Watson, 1929).

H. giganteus var. *crinitus* Nutt. Gen. II.: 177. 1818.

H. orgyalis DC. Notul. Pl. Rar. Genev., in Mem. Soc. Phys. d'Hist. Nat. Genev., 7:275. 1836. (Prod. 5:586. 1836). (T.: Cult. in Geneva Gardens, seeds from Arkansas, *Pourtales, fide* Watson, 1929.)

H. filiformis Small, Fl. S.E.U.S. p. 1265. 1903. (T.: Texas, near Dallas, *Revershon 1635*, NY!)

Roots coarse, somewhat enlarged upward; rhizomes large, elongate; stems erect, 1.5-2.5 m. tall, to 3 m. or more in cultivation, branching near the summit, glabrous, glaucous, pale green, to purple; leaves alternate, very numerous,



Map 34. *Helianthus salicifolius*

usually crowded, narrowly linear-lanceolate to linear, glabrous or with a few scattered hairs, flat, light green, midrib prominent, apex and base narrowly attenuate, entire to obscurely serrulate, sessile or subsessile, 8.0-21.0 cm. long, 0.2-1.2 cm. wide, lower-most leaves usually early deciduous, axillary fascicles usually lacking; heads usually numerous in elongate-paniculate arrangement; peduncles slender, sometimes sparsely short pubescent; phyllaries narrowly linear-lanceolate to lanceolate, long attenuate, exceeding the disk, loose but not reflexed, dark green, glabrous or slightly pubescent on backs, usually ciliolate along the margins, 1-2 mm. wide; disk 1.0-1.8 cm. in diam.; lobes of disk florets reddish-purple, nearly glabrous; chaff linear, nearly entire to shallowly 3-cuspidate, keel and tip rather closely short hirsute to ciliate; achenes slender, glabrous, 4-6 mm. long.

Chromosome number: $n = 17$

Distribution: Limestone soils, western Missouri and eastern Kansas, south to northern Texas. August-Sept.

Helianthus salicifolius is a well marked and rather uniform species, unlikely to be confused with any other sunflower. Its reddish-purple disk flowers and the very narrow leaves separate it from other perennials with which it is sympatric. Its distribution does not overlap that of *H. angustifolius* which also has dark disk flowers and narrow leaves. These two differ, however, in a number of other characters with the glabrous stems and rather long and attenuate phyllaries of *H. salicifolius* serving to separate the two most readily. The unusual plumose appearance of *H. salicifolius* resulting from the numerous, crowded, linear leaves is not unattractive, and the plant is sometimes sold as an ornamental. Watson (1929) was under the im-

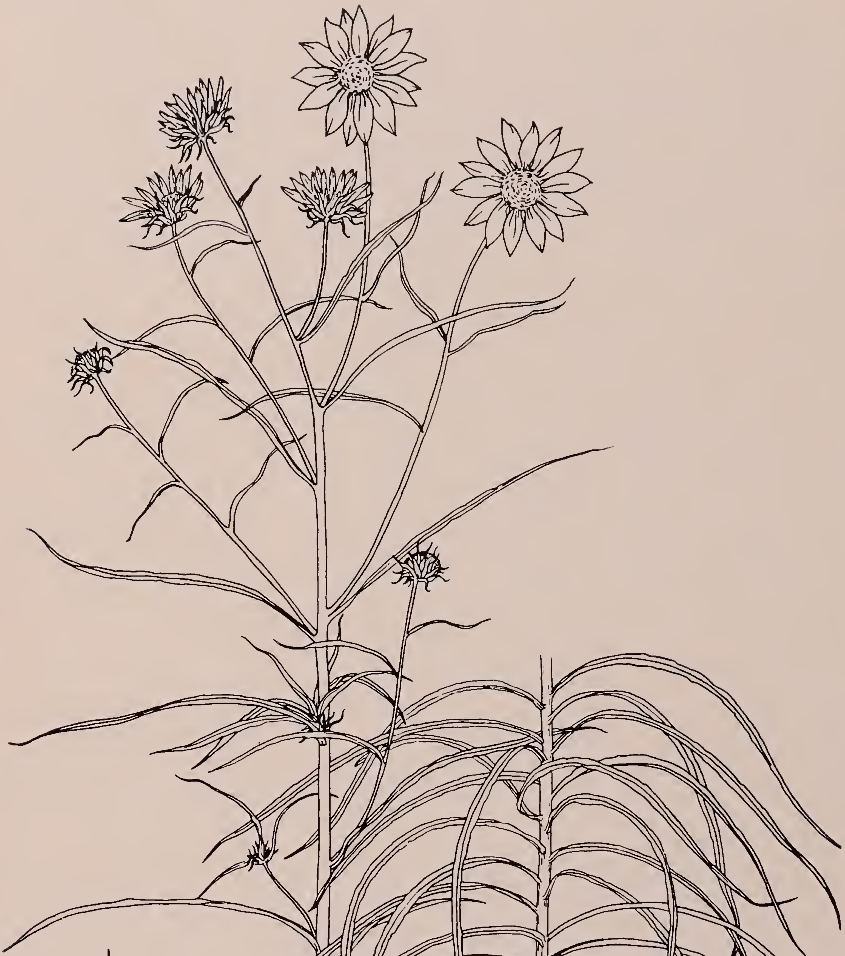


Fig. 34. *Helianthus salicifolius*

pression that it does not survive long in gardens but we have had one survive for 15 years in fairly neutral soil.

The species probably has its closest relatives in *H. grosseserratus* but it is not as close to this species as the other members of this assemblage of species are to each other. This suggested relationship tends to be borne out by results of the artificial hybridizations. Hybrids between *H. grosseserratus* and *H. salicifolius* gave pollen fertilities of 90% and a regular meiosis in one cross (Heiser, Martin and Smith 1963) although Long (1955b) secured hybrids showing lower fertility and slight meiotic irregularities. Other artificial hybrids, showing somewhat lower pollen fertilities, include those with *H. angustifolius*, *H. carnosus* and *H. giganteus* while those with *H. atrorubens* failed to produce normal flowers.

Natural hybrids do not appear to be common. A spontaneous garden hybrid has been reported with *H. maximiliani* under the name *H. orgyaloides* Ckll., and Long (1954) has listed certain herbarium specimens as putative hybrids between these species. He used the name *H.* x *filiformis* for the hybrid, although the type of *H. filiformis* appears to be a good *H. salicifolius.* The matter was further confused when we (Heiser, Martin and Smith, 1962) erroneously stated that *H. filiformis* was the same as *H. angustifolius.* Smith (1957) has seen one herbarium specimen (Ark., Logan Co., *Demaree 16033,* MO) which appears to be a hybrid with *H. divaricatus,* and *H. kellermanni* Britton appears to be a hybrid with *H. grosseserratus* (Long 1955b, 1957). However, this hybrid has not been reported to occur within the natural range of *H. salicifolius* which would mean that cultivated plants of *H. salicifolius* are involved in the parentage. Martin (1958) has listed putative hybrids with *H. angustifolius.*

A specimen collected by C. C. Parry in 1861 labeled "Colorado Territory, east of Middle Park, headwaters of Clear Creek" (GH, MO) appears to be *H. salicifolius.* However, since this collection site is far removed from all the others and also is at a much higher altitude there must be some doubt as to the accuracy of the label or my identification. Although Gray (1884) lists this species from southeastern Colorado, we have seen no other material from that state. There is also one specimen labeled "Arkansas" collected by A. Braun in 1860 (MO), and the seeds for the type of *H. orgyalis* supposedly came from Arkansas (state or river?). We have seen no other specimens from that state, although it might be expected in the western part.

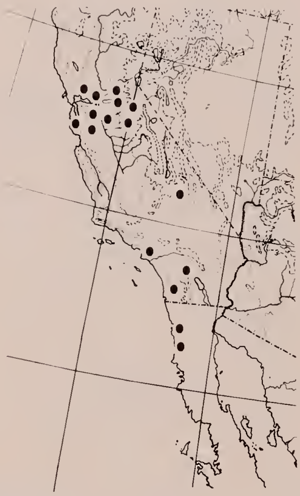
This species has become established as a weed in the Chicago area (not shown on the map. Steyermark *et al*, Rhodora 59:32. 1957.).

The type was lost during the war, and in the event no isotypes exist in Europe, *F. C. Gates 16292* from Greenwood Co., Kan. (IND, dupls. at BUT, CHI, KSC, MO) will be designated the neotype.

35. Helianthus californicus DC. Prod. 5:589. 1836. (T.: Calif., *Douglas*, K Photo, GH!)

H. californicus var. *mariposanus* A. Gray, Syn. Fl. N. Amer. 1²:277. 1884. (T.: Calif., Mariposa Co., *Bolander*, GH!)

H. giganteus var. *insulus* Kellogg, Proc. Calif. Acad. 5:17. 1875. (T.: Calif., Webb's Landing, San Joaquin R., *Kellogg* in 1872, CAS).



Map 35. *Helianthus californicus*

Perennial from much thickened woody root; rhizomes short and thick or lacking; stem 1.5-3.0 m. tall, glabrous, glaucous, sulcate; leaves mostly alternate, lanceolate, rarely ovate-lanceolate, entire or remotely serrate, hispid above, hispid to hirsute beneath, 10-20 cm. long, 2.5-6.0 cm. wide, sessile or with petioles to 3 cm. long; peduncles glabrous to hispid near summit; disks 1.5-2.5 cm. in diameter, phyllaries broadly lanceolate, 3-5 mm. wide, hispidulous to glabrous on margins, conspicuously exceeding disk in length and reflexed at maturity; lobes of the disk corollas yellow; chaff 3-cuspidate, middle cusp short acute, hispidulous; achene glabrous, ca. 5 mm. long.

Chromosome number: n = 51

Distribution: In dry, rocky soils or in wet areas, marshes and streambanks, central California and southern California extending into northern Baja California. Late July-Oct.

Although it shows considerable variation in leaf size, this sunflower is very distinct and separated from its closest relative, *H. nuttallii* ssp. *parishii* by the quite long, reflexed phyllaries. Its much larger pollen (36 microns compared to 26 microns in *H. nuttallii*) also provides a good character.

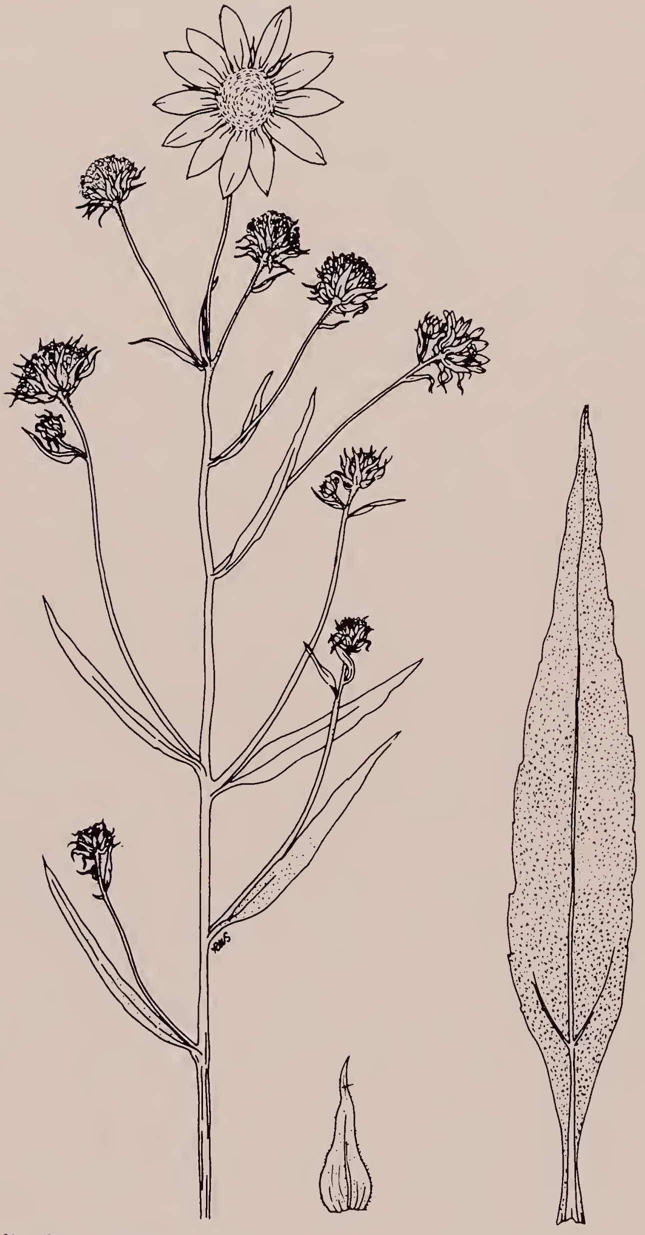


Fig. 35. *Helianthus californicus*

Although chromosome counts were obtained only from plants in the northern part of the range the pollen size was found to be uniform throughout the range, suggesting that all plants have the same chromosome number. The disjunction in the range seems to be a real one, and one might wonder if two separate origins from similar parents were involved. On both morphological and geographical grounds it seems most likely that *H. nuttallii* furnished one, or possibly two genomes. Since no tetraploid species are known in the west, it is difficult to speculate further about its origin. It is interesting to note that somewhat similar phyllaries are found in *H. resinosus*, a hexaploid of the southeast.

The type specimen appears to be rather inadequate, but de Candolle's description is sufficiently clear so that there is little doubt that the name is being attached to the proper taxon.

Material from two sources has been grown at Bloomington and although they both flowered, no seed was set on open pollination. Two plants survived one winter in the field. Artificial hybrids were secured with *H. resinosus* which although showing some quadrivalent formation gave pollen stainabilities of 98%. Seed set, however, was reduced to 15-35% of normal.

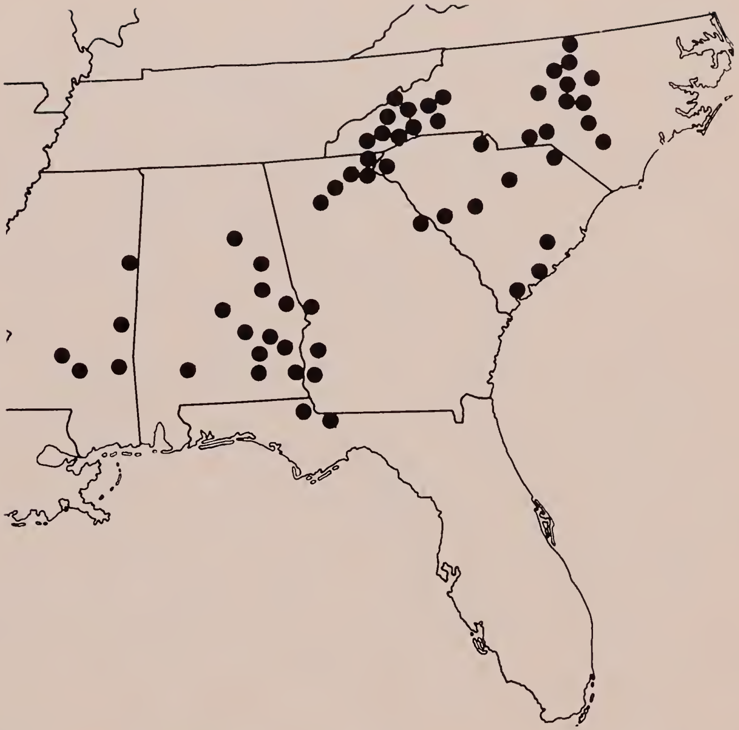
Comparison of our map with Long's (1966) reveals some differences. Apparently certain specimens from southern California which I regard as *H. nuttallii* he treated as *H. californicus*.

36. Helianthus resinosus Small, Fl. S.E.U.S., p. 1269. 1903. (T.: Fla., Gadsden Co., *Nash 2581* NY!)

(*Helianthus tomentosus* in most floras, see below)

Roots long, numerous, somewhat enlarged upward, becoming woody; rhizomes short, thick to slender; stems stout, 1-3 m. tall, green or more frequently reddish or purplish, glabrous to hispid near base, densely hispid or more frequently hirsute or somewhat villous above, usually branched above; leaves mostly alternate or at least alternate above, from narrowly lanceolate to broadly ovate, entire to serrate, scabrous, strumose or hispid above, hirsute to tomentose below and usually resin-dotted, 6.5-20.0 cm. long, 3.2-9.0 cm. wide, decurrent on petiole and hence sessile or with petioles to 2 cm. long; heads on short, stout peduncles; disks (1.5-) 2.0-2.7 cm. in diam.; phyllaries narrowly to broadly lanceolate, acute to long attenuate, hispid to white villous, usually glandular, usually much longer than disk and somewhat squarrose, 3-5 mm. wide; rays light yellow to rarely deep yellow, 1.8-2.5 cm. long; chaff 3-cuspidate, tip densely pubescent or rarely nearly glabrous; achenes glabrous, 5-7 mm. long.

Chromosome number: $n=51$



Map 36. *Helianthus resinosus*

Distribution: North Carolina to northwest Florida to Mississippi. (May-) July-Sept. (-Oct.).

This is a fairly "good" species among the polyploid sunflowers but shows considerable variation, particularly in regard to leaf size and shape, as was pointed out by Watson (1929). The best characters distinguishing it from other southeastern sunflowers are found in the heads which are usually quite large and with generally rather broad phyllaries which are recurved at maturity. The pubescence of the leaves and their mostly alternate arrangement also serve to separate it from *H. tuberosus* and *H. strumosus* with which it may at times be confused. Although not much field study has been devoted to this species, the examination of herbarium specimens suggests that some of the variation may result from hybridization with *H. strumosus* and *H. tuberosus*, although the latter species is rare in the southeast. Watson's report of tubers in this species, which does not hold for the material grown at Bloomington could, of course, result from hybridization with *H. tuberosus*. There is no evidence of hybridization with *H. schweinitzii* which falls within its geographical range. Artificial hybrids were quite readily secured with

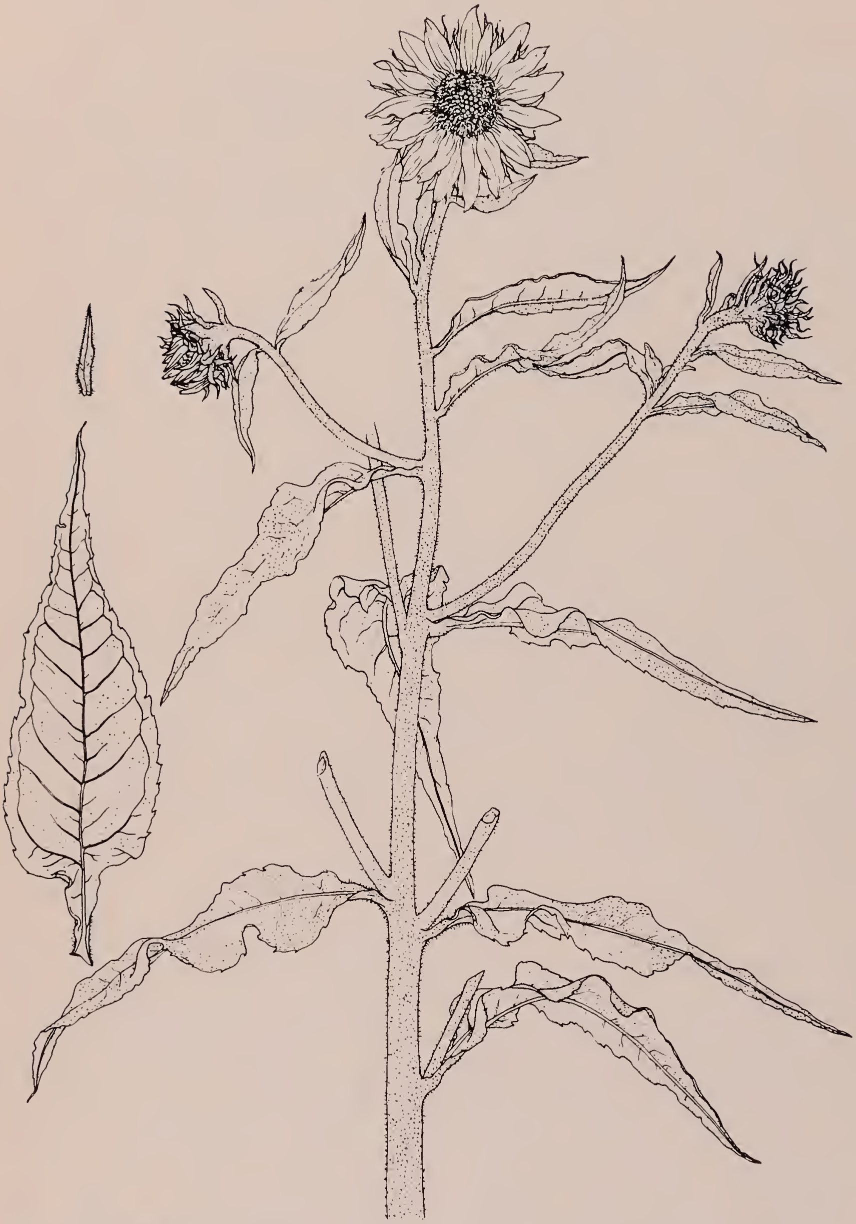


Fig. 36. *Helianthus resinosus*

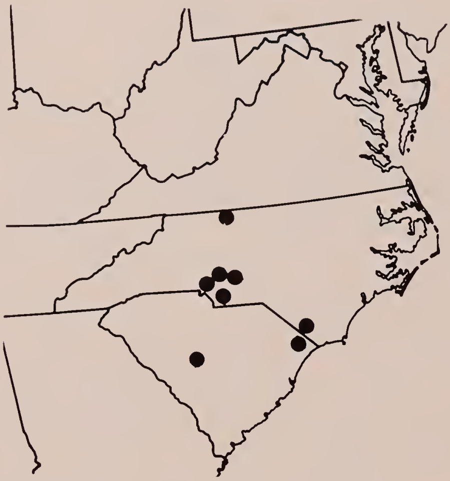
H. schweinitzii, *H. strumosus*, and *H. tuberosus* and, after several attempts, with *H. californicus*.

As to the origin of this hexaploid species, *H. giganteus* and *H. mollis* appear to be the most likely candidates to have furnished genomes. Since both of these species are diploid insofar as is known, this would account for only two of the three genomes in *H. resinosus*, unless one of these species contributed two genomes. This species might perhaps be equally well placed in the series Divaricati; the reason for placing it in the Gigantei is the prevailing alternate arrangement of the leaves.

Since the time of Elliott's work (1824) this species has been called *Helianthus tomentosus* in various floristic treatments. Watson recognized both *H. tomentosus* and *H. resinosus* but there can be little question that these both belong to a single, although variable, species. Michaux gives Illinois as the type locality for his *H. tomentosus* and his description seems to match most nearly that of *H. tuberosus*, although Cronquist (in Gleason, 1952) suggests that he may have been referring to a plant similar to *H. giganteus*. In any event, it is clear that the name *H. tomentosus* cannot be applied to the southeastern species. Under the synonymy of *H. tomentosus*, Watson (1929) lists both *H. spathulatus* Ell. and *H. squarrosus* Nutt. Elliott describes *H. spathulatus* as having opposite leaves, entire chaff, and phyllaries as long as the disk, and presumably it had spathulate leaves, whereas the species in question nearly always has alternate leaves, at least above, tricuspidate chaff, phyllaries exceeding the disk in length, and lanceolate to ovate leaves. Moreover, Elliott does not associate his *H. spathulatus* with *H. tomentosus*. Thus, although I am at a loss to suggest the identity of *H. spathulatus*, it apparently is not the same as this species. *Helianthus squarrosus* Nutt. is a later homonym of *H. squarrosus* HBK. (=*Viguiera linearis* (Cav.) Sch. Bip.) and hence is not available. Since Nuttall states that his species was "*H. tomentosus* Elliott, non Michaux" he was the first to recognize the misapplication of this name. Jackson (1953) has also placed *H. pilosus* Tausch (Fl. 11:502. 1828) in synonymy under *H. tomentosus* but this name almost certainly refers to a hybrid of *H. mollis* with some other species, probably *H. giganteus*, which seems likely since both of these were grown in Europe at this time and *H. pilosus* is of garden origin. Thus, we are left with Small's *H. resinosus* as the only name available for the plant that has generally been called *H. tomentosus*.

37. Helianthus schweinitzii T. & G. Fl. N. Am. 2:330. 1841. (T.: North Carolina, *Schweinitz* GH!)

Roots clustered, quite tuberous; rhizomes short; stems 1.0-2.0 m. tall, strigose to short hispid-hirsute below, strigose to glabrous above, frequently deep red, sparingly to much branched above; leaves opposite below,



Map 37. *Helianthus schweinitzii*

usually becoming alternate above, lanceolate to linear-lanceolate, acute to acuminate, revolute, entire or with a few small teeth, occasionally slightly undulate, scabrous above, tomentose to short hirsute below, to 14 cm. long, 2.0 cm. wide, usually much smaller, petioles to 3.0 cm. long or leaves more frequently sessile or subsessile; heads usually few; disks 0.9-1.6 cm. in diameter; phyllaries lanceolate, ca. 2 mm. wide, equalling to slightly exceeding disk, loose, sometimes slightly squarrose, acute to acuminate, short-hirsute near base, nearly glabrous above; rays 15 or less, to 2.2 cm. long; disk corollas yellow; chaff 3-cuspidate, middle cusp acute, ciliate to hispid; achene glabrous, 3-4 mm. long.

Chromosome number: n = 51

Distribution: North and South Carolina.

Watson did not clearly designate the type of this species, therefore the Schweinitz specimen in the Gray Herbarium is so designated. Smith annotated this as "*H. microcephalus* x *giganteus.*" The specimen which Martin labeled *H. angustifolius* x *atrorubens* (*Godfrey 6263*, GH, US) also probably should be referred to this species.

The most distinctive feature of *H. schweinitzii* is its tuberous roots but unfortunately these are not always collected. The aerial portion of the plant does not have many distinctive features and could be confused with *H. floridanus*, *H. resinosus* and *H. strumosus.* However, the relatively small heads, the rather narrowly lanceolate leaf which is revolute (at least when dry) and rather densely pubescent on the lower surface combine to serve to separate it from other species.

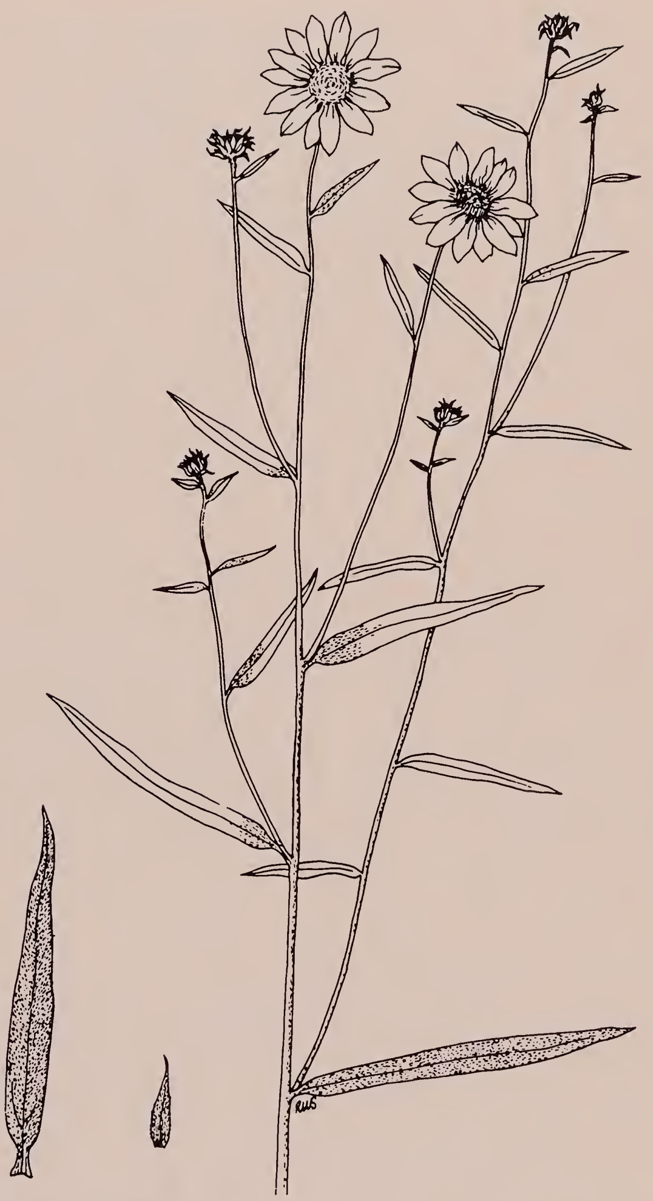


Fig. 37. *Helianthus schweinitzii*

Since this species is a hexaploid, Smith's annotation is suggestive of its origin. The small heads could be derived from *H. microcephalus* and the tuberous roots from *H. giganteus*. The slightly revolute lanceolate leaf also suggests the possibility of a genome from *H. angustifolius* or *H. floridanus*.

This species has one of the most restricted distributions of any hexaploid species, as here recognized, in the genus, and as Watson pointed out is a rather rare species. Fertile artificial hybrids have been obtained in crosses with both *H. resinosus* and *H. tuberosus*.

Series 3. Microcephali

Roots fibrous to coarse, not tuberous; rhizomes lacking, poorly developed, or short and thick; stems glabrous, often glaucous; stem leaves well developed except in *H. longifolius*, becoming alternate above; disks small (mostly 0.8-1.5 cm. in diam.); lobes of disk corolla yellow; achenes 2-4 mm. long.

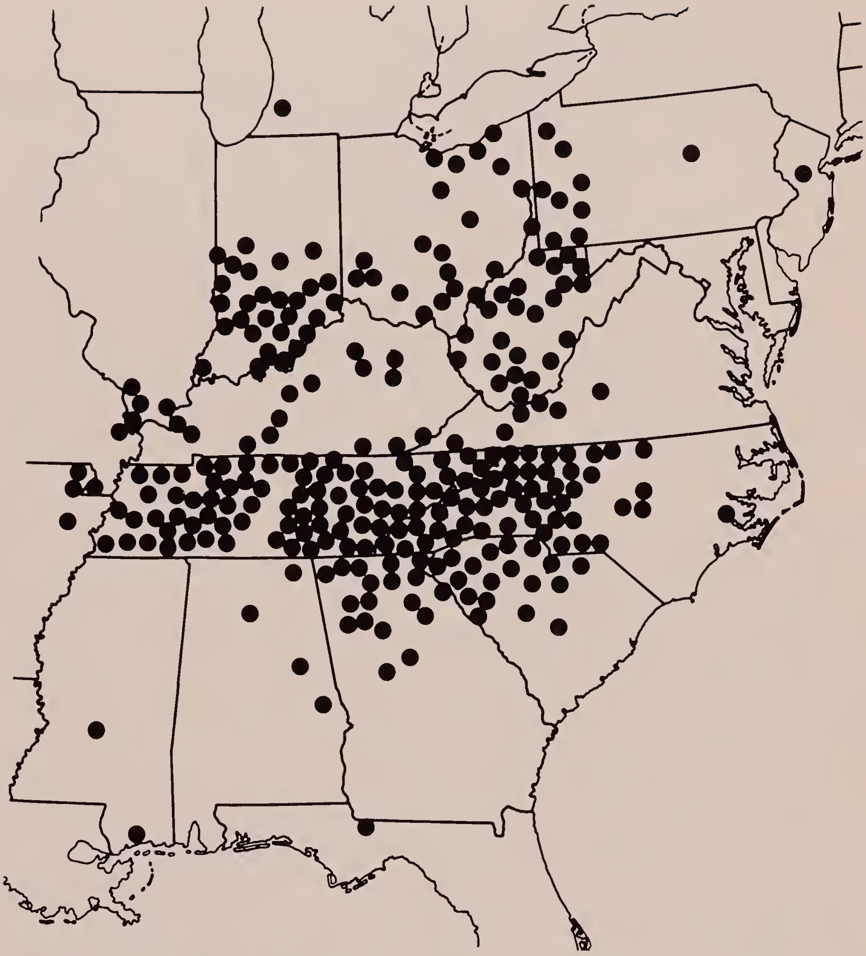
Key to Species of Microcephali

Leaves tomentulose to nearly glabrous below and resin dotted, petiolate.
  Leaves lanceolate to ovate with petioles frequently longer than 1.5 cm., tomentulose beneath; wide-spread in eastern United States........................38. *H. microcephalus*
  Leaves narrowly lanceolate to linear-lanceolate with petioles less than 1.5 cm. long, nearly glabrous below; Georgia..................................41. *H. smithii*
Leaves glabrous or nearly so below, not resin dotted, subsessile to petiolate.
  Leaves glaucous beneath, lanceolate; basal rosettes lacking.
    Leaves distinctly petiolate; Tenn. and N.C.....................39. *H. glaucophyllus*
    Leaves usually sessile or subsessile; Va., W.Va., and N.C...........40. *H. laevigatus*
  Leaves not glaucous beneath, linear to narrowly obovate; basal rosettes usually present...42. *H. longifolius*

38. Helianthus microcephalus T. & G. Fl. N. Am. 2:329. 1842. (T.: "Upper Canada," *Goldie*, K photo, IND)

H. divaricatus var. *ferrugineus* Ell. Sketch 2:420. 1824.
H. strumosus var. *pallidus* Ell. Sketch 2:420. 1824.
H. parviflorus Bernh. ex. Spreng. Syst. 3:617. 1826 (not HBK.)
H. pallidus Farwell, Asa Gray Bull. 3:21. 1895.

Roots fibrous, crown buds abundant; stems 1.0-2.5 m. tall, stout or slender, usually very ramose, glabrous, commonly brown and glaucous; leaves opposite below, becoming alternate about the middle of stem, lanceolate to ovate, rounded to cuneate at base, tapering to petiole 1.0-3.5 cm. long, acuminate at tip, margin subentire to moderately serrate, grayish-tomentulose with numerous resin-dots beneath, scabrous above, triple-veined, the lateral veins alternate, diverging 1.0-3.5 cm. from leaf base, 7.0-18.0 cm. long and



Map 38. *Helianthus microcephalus*

2.0-6.0 cm. wide; heads few to many; peduncles elongate, slender, ascending; disk 0.6-1.0 cm. in diam.; rays 5-8, pale to deep yellow, 1.0-1.5 cm. long; phyllaries equalling to slightly exceeding disk, narrowly lanceolate, acuminate, erect or squarrose, loose, glabrous or nearly so on back, margin ciliolate, 1.5-2.5 mm. wide; pales shallowly three cuspidate, pubescent on tip; achenes 2.0-3.5 mm. long.

Chromosome number: n = 17

Distribution: Abundant in semi-open woods, partially shaded roadsides, and cut-over woodland. New Jersey to southern Michigan to northeastern Arkansas, south to northern Florida and Alabama. Aug.-Sept.

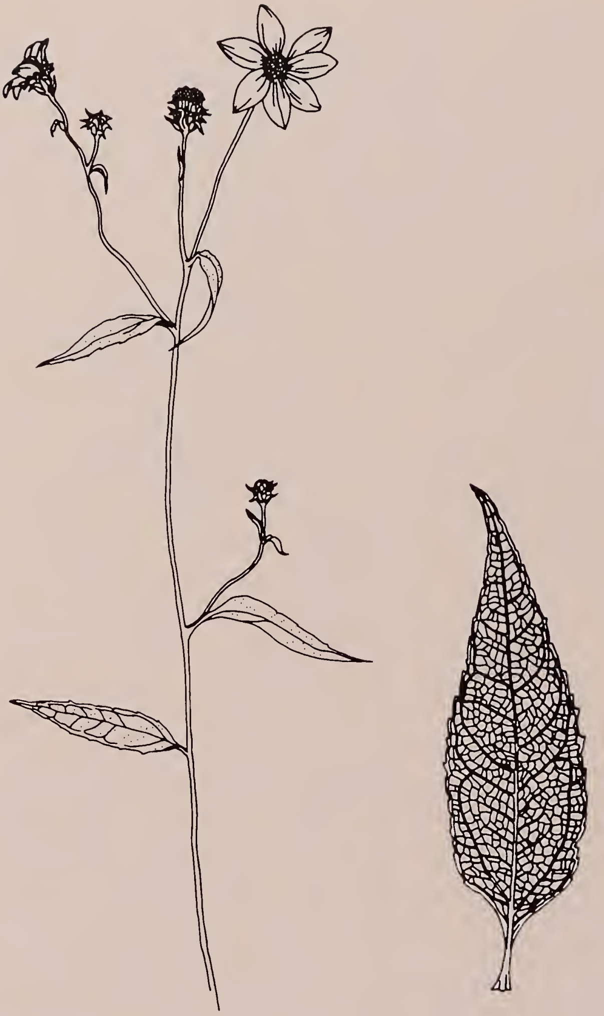


Fig. 38. *Helianthus microcephalus*

This rather aptly named sunflower is quite variable but is well set off from most other species by its small heads, glabrous stems, petiolate leaves as well as its "preference" for shade. It is most likely to be confused with *H. glaucophyllus* to which it appears most closely related, although the strongly tomentulose lower leaf surface of *H. microcephalus*, as opposed to the glabrous and glaucous leaf of the *H. glaucophyllus*, serves readily to distinguish them. It seems likely that one or the other or both of these species is involved in the origin of the small headed polyploids.

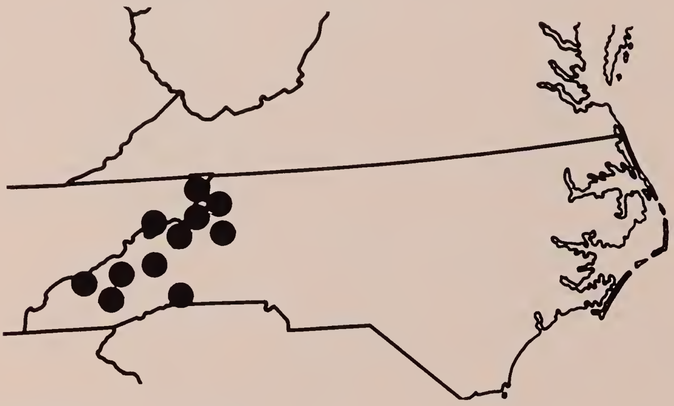
Although on morphological grounds this species does not appear particularly close to *H. divaricatus*, the two hybridize freely in many areas (Smith and Guard, 1958) producing *H. glaucus* Small. The artificial hybrid between the two species is difficult to obtain but is rather highly fertile. Other artificial hybrids have been secured with *H. atrorubens* (erroneously reported as a natural hybrid in Heiser, Martin and Smith, 1962), *H. giganteus*, *H. glaucophyllus*, *H. longifolius*, and *H. mollis*.

An interesting collection made by Janice Beatley in DeKalb Co., Tenn. (25461, IND.) was identified by her as "*H. microcephalus* x *eggertii*" and two of the four plants showed high pollen stainability. In view of the fertility and the fact that one putative parent was a diploid and the other a hexaploid, I was not fully convinced of the hybrid origin, although the plants could be referred to no other species and did combine characters of the two putative parents. Seeds taken from one of the herbarium specimens gave rise to two plants (*Heiser H511*) which were tetraploid. Neither plant was quite like the parent, one having broadly lanceolate leaves, glabrous beneath, approaching *H. glaucophyllus* in appearance and the second having narrowly lanceolate leaves, somewhat hispid beneath, approaching a small-headed *H. strumosus*. In view of the chromosome number and the segregation observed in the progeny I feel that Beatley's determination of this as a hybrid or hybrid derivative of *H. microcephalus* and *H. eggertii* is probably correct. This example serves well to illustrate the difficulties inherent in trying to arrive at an understanding of the perennial sunflowers.

For a discussion of the synonymy of the species the reader is referred to Torrey and Gray's original description. They cite Goldie's specimen from Canada first in giving the geographical range of the species. Because this specimen was cited first, Watson (1929) accepted it as the type although he did not see it. A photograph of this specimen has been examined and as far as can be judged from a photograph it appears to be "good" *H. microcephalus*. However, the geographical source given is outside the range of the species as it is now known. There is no compelling reason, it would appear, to regard the Goldie specimen as the holotype and it may prove desirable to designate a lectotype. However, this should not be done until an actual examination of the specimen is made. The variety *gamma* of Torrey and Gray is based on

"Drummond" from Covington, La. This specimen, perhaps at New York, has not been seen and therefore satisfactory deposition cannot be made. Since Louisiana is outside of the known range of this species, it may prove to be some species other than *H. microcephalus*.

39. Helianthus glaucophyllus D. M. Smith, Brittonia 10:142. 1958. (T.: North Carolina: Avery Co., *Smith 1075* IND!)



Map 39. *Helianthus glaucophyllus*

Roots fibrous; rhizomes short, crown buds numerous; stem 1.0-2.0 m. tall, slender, green or dark brown, usually glaucous, glabrous; leaves opposite below, becoming alternate above, lanceolate, abruptly narrowed at base, acuminate at tip, triple veined, the lateral veins usually alternate, diverging 1.0-3.0 cm. from leaf base, 9.0-18.0 cm. long, and 3.0-7.0 cm. wide, and margin moderately to deeply and sharply serrate, remotely scabrous above, entirely glabrous and conspicuously glaucous beneath; gradually tapering to petiole, 1.0-3.0 cm. long, heads few-many; peduncles long, slender, ascending; disk 0.9-1.3 cm. broad; rays 5-8, pale yellow, about 1.5 cm. long; phyllaries slightly exceeding disk, attenuate, mostly erect, glaucous, ciliolate on margin; pales shallowly three cuspidate, pubescent near tip; achenes ca. 4 mm. long.

Chromosome number: $n = 17$

Distribution: Moist forests and shady roadsides, generally above 2500 feet in the Blue Ridge and Smoky Mountains of North Carolina and Tennessee. Aug.-Sept.

This species appears to be closely related to *H. microcephalus* and is distinguished from it by the glabrous, glaucous lower leaf surface, the slightly larger heads, and the broader and slightly longer phyllaries. From *H. laevigatus* it is readily separable by the longer petioles. Artificial hybrids with high fertility were secured with *H. microcephalus*, but natural hybrids

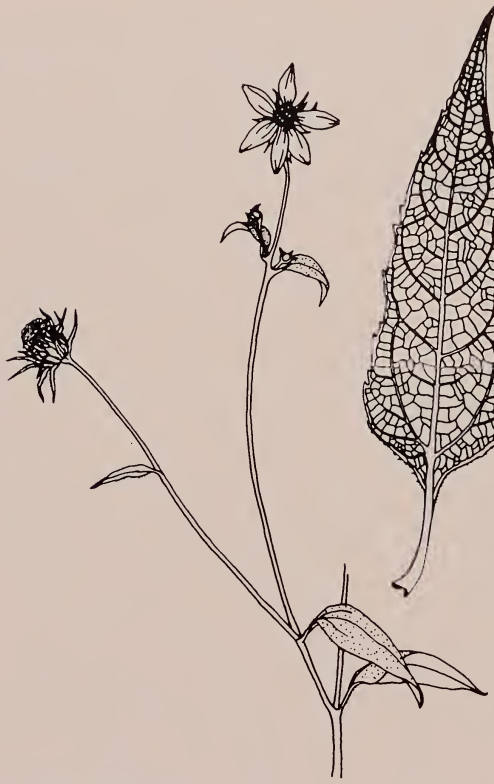
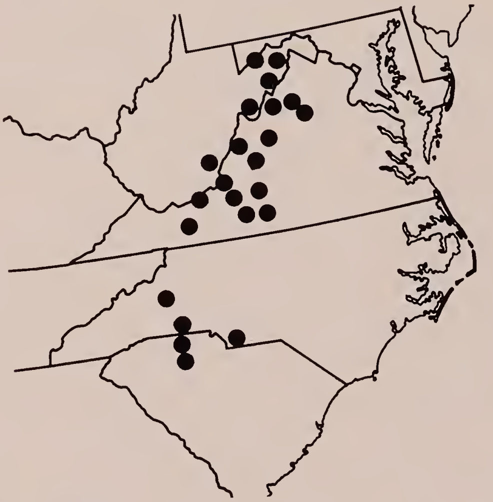


Fig. 39. *Helianthus glaucophyllus*

of this species thus far are unknown. This species grows within the area of *H. microcephalus* but apparently always occurs at higher elevations. There might be some justification for considering it a subspecies of *H. microcephalus* but in the present context it is clearly a species. An isotype is deposited at the University of Kentucky.

40. Helianthus laevigatus T. & G. Fl. N. A. 2:330. 1842. (T.: collection without label, NY!)

H. laevigatus ssp. *reindutus* Steele, Contr. U.S. Nat. Herb., 13:374. 1911. (T.: Virginia: Bath Co., *Steele*, US!)
H. reindutus E. E. Wats. Pap. Mich. Acad. Sci. 9:376. 1929.



Map 40. *Helianthus laevigatus*

Roots coarse; rhizomes short, stems 1.0-2.2 m. tall, slender, usually branched above, glabrous or rarely hirsute at base, often glaucous; leaves opposite below, becoming alternate above middle, lanceolate, acuminate, narrowed to subsessile base, faintly 3-veined, the two lateral veins diverging 1.0-2.0 cm. from base of leaf, essentially glabrous and subcoriaceous, regularly serrate to subentire, 8.0-15.0 cm. long, 1.5-3.5 cm. wide; heads 1-several on slender peduncles; disk 1.0-1.5 cm. in diam.; phyllaries loosely imbricate, equalling or slightly exceeding disk, more or less erect, linear-lanceolate, acuminate-attenuate, glabrous on back, margins sometimes ciliate, 2-3 mm. broad; rays 5-10, narrow, 1.5-2.0 cm. long; pales obscurely three cuspidate, somewhat pubescent at tip; achene ca. 4 mm. long.

Chromosome number: n = 34

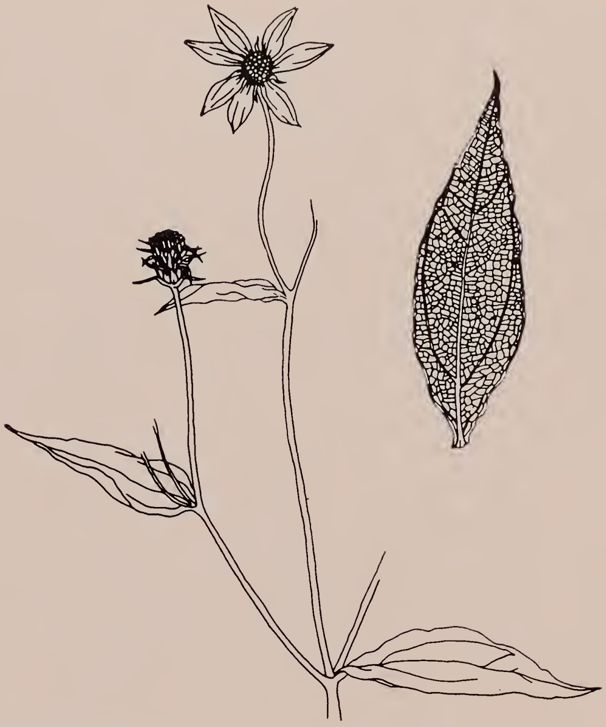


Fig. 40. *Helianthus laevigatus*

Distribution: Relatively common in shale-barrens of Allegheny Mountains of Virginia, West Virginia, and North Carolina. Aug.-Sept.

Unlike the other tetraploids of eastern North America, *H. laevigatus* is quite well marked and does not intergrade with other species. In fact, the only species known to grow near it is *H. divaricatus.* Although natural hybrids are unknown, artificial hybrids have been secured with *H. decapetalus* (4n) and show high pollen stainability and fair seed production.

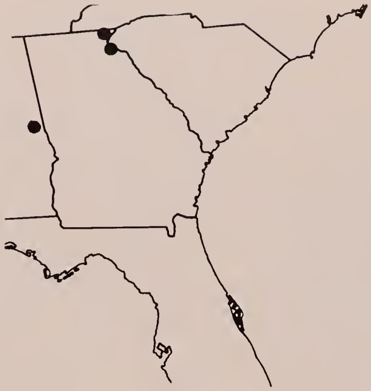
The species is restricted to a very limited area of the Appalachians, for the most part confined to outcrops of Devonian shale, referred to as "barrens." Steele (1911), Wherry (1930) and Allard (1946) have called attention to the large number of endemics in this area. Watson (1929), Fernald (1950) and Gleason (1952) all list this species as occurring in Pennsylvania but no specimens are known from that state.

The relatively small heads of the species in combination with the sessile or subsessile glabrous leaves fairly readily separate this species from other eastern sunflowers. Contrary to Watson's (1929) statement, there are reasons for considering the species related to *H. longifolius.* The shape and size of the heads and the cauline leaves of the two are somewhat similar. Although these two species are fairly widely separated geographically today, it is conceivable that *H. longifolius* contributed one genome to this species. Another species possibly involved in its origin is *H. glaucophyllus* which replaces it to the south. *Helianthus laevigatus* also shows morphological similarities to certain hexaploid forms of *H. strumosus* and to *H. eggertii.* It is, of course, possible that *H. laevigatus* crossed to certain diploid species to produce hybrids which when the chromosome number was doubled produced certain races of these hexaploids.

Steele's *H. laevigatus* ssp. *reindutus* is characterized by bearing a few scattered trichomes on the leaves and stems, hardly sufficient basis for taxonomic recognition.

41. **Helianthus smithii Heiser,** Rhodora 66:346. 1964, based on *H. parviflorus* var. *attenuatus* A. Gray, Syn. Fl. N. Am. 1^2:278. 1884. (T.: Georgia, Rabun Co., *Donnell Smith* 6, GH!)

Roots coarse; rhizomes short, thick, numerous crown buds present; stems 0.7-1.5 m. tall, branched, glabrous or nearly so, glaucous, purplish; leaves mostly opposite, becoming alternate above, narrowly lanceolate to linear-lanceolate, attenuate, serrulate, one nerved, scattered strumose-hispid above, lighter green to glaucous below with a few scattered hairs and resin dotted, to 18 cm. long by 1.8 cm. wide, gradually narrowed to a short but distinct petiole to 1.3 cm. long; heads several on very slender peduncles; disks 0.5-1.5 cm. in diam; phyllaries lanceolate, all shorter than disk or some exceeding disk, reflexed, ciliate on margin, glabrous or with a few scattered hairs on



Map 41. *Helianthus smithii*

back, 1.0-2.0 mm. broad; rays 6-9, to 1.2 cm. long and 0.4 cm. wide; pales entire, villous on back; achene 3 mm. long.

Chromosome number: n = 34

Distribution: Known only from northeastern Georgia and eastern Alabama, dry soils in open woods. Aug.-Sept.

This is apparently a rare sunflower. In addition to the type it is known from a collection from Randolph Co., Alabama (*Smith 1842, K44*, IND) and from Stephens Co., Georgia (*F. H. Sargent* 95, US). A collection from Barstow Co., Georgia (*Duncan 8849*, IND, MO, US) approaches this species in several characteristics but has slightly larger heads and longer, more slender rhizomes. In June of 1960 I visited the type locality. A colony of young sunflowers was found along highway No. 441 and rhizomes were collected. Plants (*Heiser 4658*) grown from these proved to be hexaploid, and although having relatively narrow leaves and moderately small heads probably should be referred to *H. strumosus*. It is, of course, possible that *H. smithii* still occurs in the type area but that I failed to locate it.

The very narrow short-petiolate leaves and the small heads of the species serve fairly readily to distinguish it from other species of the area. It is difficult to suggest what species might be involved in its origin—the small heads and the resin dots on the leaves suggest *H. microcephalus*. The narrow leaves perhaps might come from either *H. longifolius* or *H. angustifolius*, although it has few other characters that can be associated with these species.

Vigorous, rather fertile hybrids have been secured with three other tetraploid species, *H. decapetalus*, *H. hirsutus*, and *H. strumosus*, and hybrids have also been secured with three hexaploids, *H. resinosus*, *H. schweinitzii*, and *H. strumosus*. Only one hybrid was obtained in crosses with the first two species, but numerous hybrids were obtained with *H. strumosus*. Eight

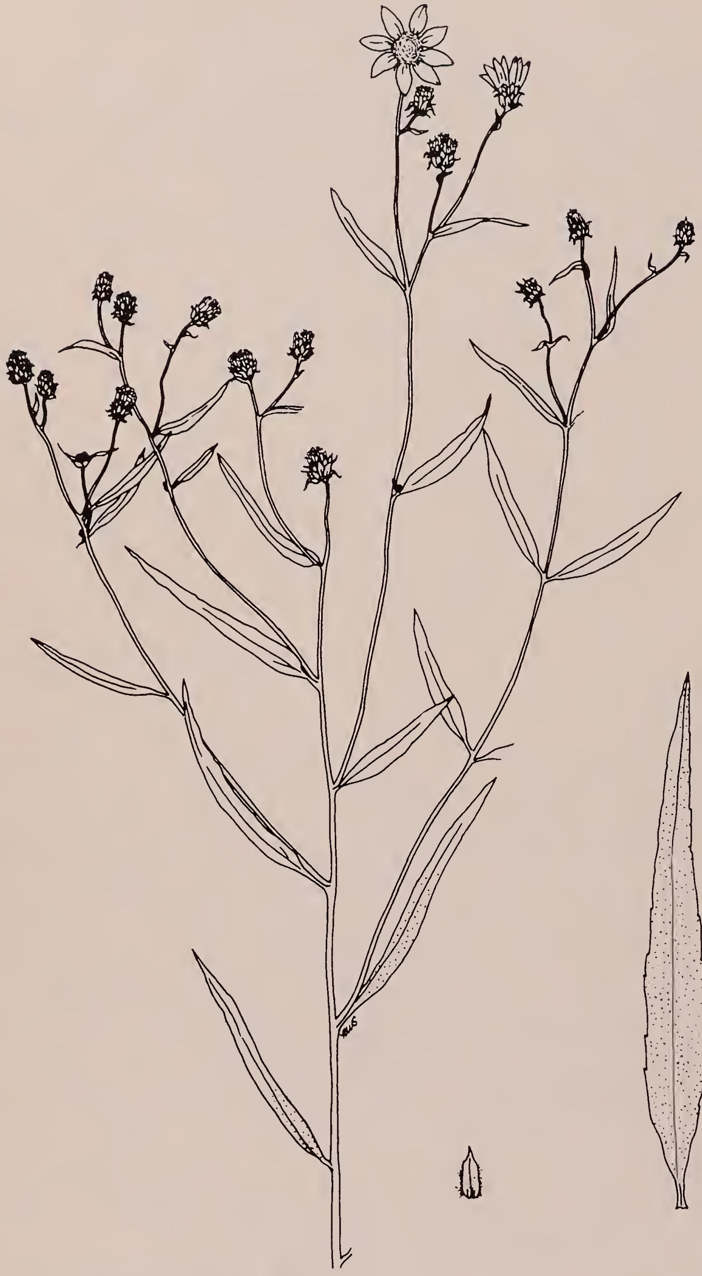
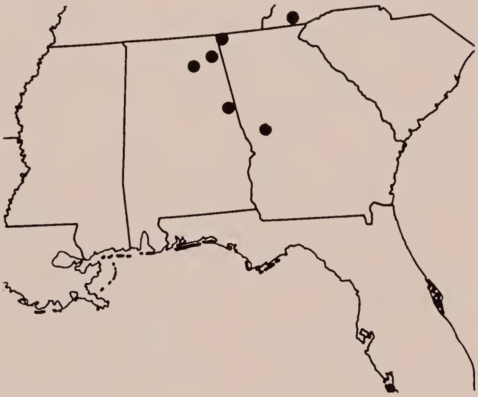


Fig. 41. *Helianthus smithii*

of these were grown to maturity, gave pollen stainabilities of 83-99% and showed some seed set.

42. **Helianthus longifolius Pursh,** Fl. Am. Sept. 2:571. 1814. (T.: western parts of Georgia, *John Lyon*, location unknown) not *Helianthus longifolius* Hook. Fl. Bor. Am. I. 313. 1840 = *Wyethia angustifolia* (DC.) Nutt.

Leighia longifolia Nutt. Trans. Am. Phil. Soc., N.S., 7:365. 1841.



Map 42. *Helianthus longifolius*

Roots slender, rhizome poorly developed or lacking; stems several, erect, green to purplish, 0.5-1.2 m. tall, little branched above, glabrous; basal leaves in rosettes, linear to elongate-lanceolate or narrowly obovate, flat, entire or rarely obscurely serrate, glabrous, 3-nerved but lateral nerves sometimes obscure, light green, 13.0-30.0 cm. long, 0.7-2.0 cm. wide, long petiolate to subsessile; cauline leaves resembling basal leaves but shorter, more frequently sessile, sometimes clasping, opposite, becoming alternate in inflorescence of well-developed plants; heads few to several, disk .9-1.2 cm. in diam; phyllaries linear-lanceolate, short to long attenuate, outer sometimes loose or recurving, equalling or exceeding disk, glabrous or with a few scattered hairs, 1.0-1.8 mm. wide; rays light yellow to yellow, 12-14 mm. long; pales thin, three-cuspidate; achenes 2.0-2.5 mm. long.

Chromosome number: n = 17

Distribution: In dry, rocky soil, southwestern North Carolina, western Georgia, and northeastern Alabama. Sept.-Oct.

This species, as is true of most species of the genus having a restricted range, is rather distinctive, and shows relatively little variability. It does not appear to be particularly closely related to any other species, although

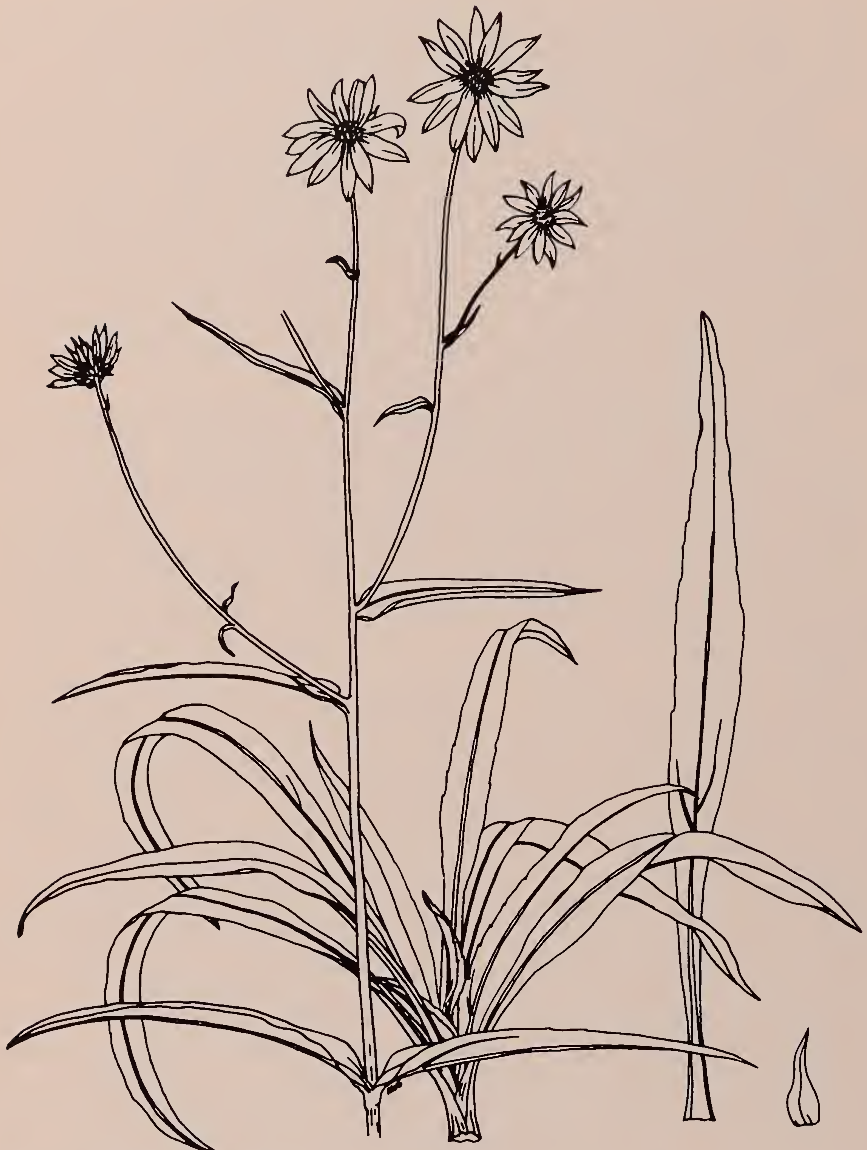


Fig. 42. *Helianthus longifolius*

in vegetative features it is somewhat similar to *H. carnosus.* The larger head and broader phyllaries as well as the scapose appearance of the latter readily serve to distinguish the two.

Artificial hybrids have been secured with *H. angustifolius, H. carnosus, H. floridanus, H. maximiliani, H. mollis, H. microcephalus, H. occidentalis,* and *H. silphioides.* Somewhat unusual for the eastern perennials is the fact that these hybrids generally showed less than 50% pollen stainability, and an even more highly reduced seed set. Meiosis, however, generally revealed 17 pairs in most of the hybrids that have been examined. A search of an area containing both *H. microcephalus* and *H. longifolius* failed to reveal any natural hybrids; natural hybrids with both *H. atrorubens* and *H. occidentalis* are known (Smith and Martin, 1959).

A misconception about the habitat of this species has been carried in the literature since Elliott (1824) emended Pursh's original description. Elliott stated that this species grew in damp, rich soils, and later Watson (1929) mentioned that *H. longifolius* grew only in very wet soil. Watson apparently had not collected this species, however, since he mentioned that he was unsuccessful in locating it in its type locality. Martin and Smith have collected this species in three areas and have never found it in other than dry, rocky habitats.

There are also some discrepancies between the original description and that now given for the species. The original description reads "glaberrimus; caule paniculato, ramis summitate paucifloris, foliis subsessilibus longissime-lanceolatis tripinervibus intergerrimis, inferioribus serrates, calycinis squamis ovatis acutis, exterioribus linearibus divaricatus. . . . From four to seven feet high; stem dark purple and very smooth; flowers middle size."

Helianthus longifolius, as now interpreted, agrees very well with the glabrous condition, the paniculately branched stem, the few-flowered branches toward the top, the subsessile, elongate-lanceolate, three-nerved, entire leaves, the dark purple, very smooth stems and perhaps the middle sized flowers of Pursh's description. However, the lower leaves of *H. longifolius* are seldom somewhat serrate, the phyllaries are not ovate-acute, and all the specimens seen have been three feet or less in height. Pursh does not mention the habitat of this plant. The possibility of the type locality being low and wet may have some bearing on the greater height of the original specimen, although greenhouse grown plants have never exceeded three feet in height.

Thus it seems possible that Pursh may have been describing some other species or a hybrid. No other species seems to fit his description. Hybrids with *H. atrorubens* may have somewhat ovate bracts but are seldom much taller than three feet and do not have serrate leaves. Thus, although there is some uncertainty in the assignment of the name *H. longifolius,* there is hardly sufficient reason to give up this long used name, particularly so in view of the fact that a detailed search might reveal the type is no longer extant. In that event, *R. M. Harper 3237* from Talbot Co., Georgia, (NY with duplicates at GH, US) will be designated the neotype.

Series 4. Angustifolii

Roots fibrous to coarse; rhizomes lacking to well developed; stems pubescent; basal leaves often differing in shape from stem leaves; latter usually alternate and somewhat revolute; phyllaries mostly 1-2 mm. broad; disks small to medium sized; lobes of disk corolla yellow or purple; achenes 2-3 mm. long; mostly species of southeastern United States.

Key to Species of Angustifolii

Leaves not conspicuously undulate; outer phyllaries acute to slightly acuminate.

Leaves usually strongly revolute, linear to lanceolate, usually more than 5 times as long as broad, seldom over 8 mm. wide; rhizomes poorly developed or lacking .... 43. *H. angustifolius*

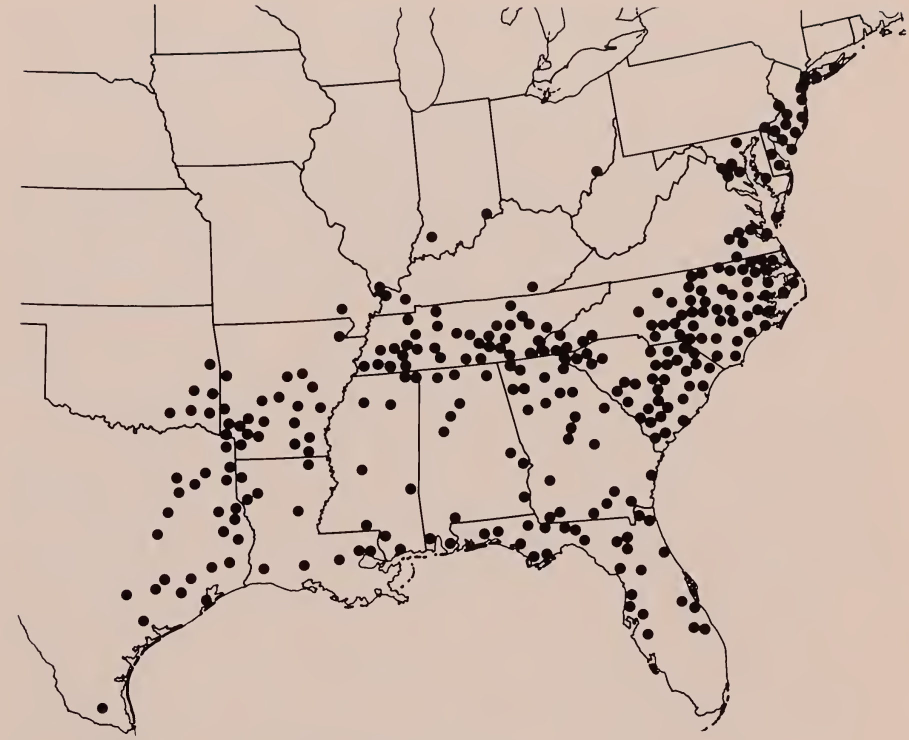
Leaves flat to weakly revolute, narrowly to broadly lanceolate, usually over 8 mm. wide; rhizomes well developed .... 44. *H. simulans*

Leaves usually undulate, lanceolate to ovate, rarely more than 5 times as long as broad; outer phyllaries often obtuse .... 45. *H. floridanus*

43. Helianthus angustifolius L. Sp. Pl., 906, 1753. (T.: Virginia, *Clayton*)

Coreopsis angustifolia L. Sp. Pl., 908. 1753. (T.: Virginia, *Clayton*)
Rudbeckia angustifolia L. Sp. Pl., ed. 2, 1281. 1763.
Leighia bicolor Cass. Dict., 25:436. 1826.
H. polyphyllus Small, Bull. Torrey Bot. Club, 25:480. 1898. (Dekalb Co., Ga. *Small s.n.*, NY!)
H. angustifolius var. *nemorosus* Mohr, Contr. U.S. Nat. Herb. 6:800. 1901. (T.: Mobile Co., Alab. *Mohr s.n.* US!)
H. angustifolius var. *planifolius* Fern. Rhodora, 49:190. 1947. (T.: Sussex Co., Va. *Fernald & Long 11470* GH!)

Roots fibrous; rhizomes short and slender or lacking; crown buds abundant; stem 0.5-1.5, rarely 2 m., tall, simple or often much branched above, usually strigose or hispid above, hirsute near base, rarely glabrous or nearly so; axillary fascicles sometimes present; basal leaves ovate, oblanceolate or spatulate, narrowed to a short petiole, usually absent at flowering; cauline leaves usually numerous, not crowded, mostly alternate, sessile, firm, linear to narrowly lanceolate or rarely narrowly ovate, as much as 18 cm. long and 1.8 cm. wide, generally 8-10 cm. long, 3-5 mm. wide, very variable but usually not more than one-tenth as wide as long, margins usually strongly revolute, dark green and scabrous above, much lighter beneath, nearly glabrous to tomentose, midrib prominent; heads on slender, hispid peduncles 5 to 16 cm.



Map 43. *Helianthus angustifolius*

in length; phyllaries narrowly lanceolate to lanceolate, loose, acute or slightly acuminate to short attenuate, scabrous, or rarely glabrous, outer row shorter and more acute, inner row seldom longer than the disk, 1-2 mm. wide; rays 10-20, 1.0-2.0 (-2.5) cm. in length, lobes of disk corollas purple, rarely yellow; style branches usually yellow; anthers black; pales 3-cuspidate, lateral cusps short and obscure, achenes slender, 2-3 mm. long.

Chromosome number: n = 17

Distribution: New York to Florida, west to Oklahoma and Texas; usually in moist, shady places but known from a variety of habitats.

Throughout most of its range *H. angustifolius* is a very clear cut species, although like most of the widespread species it shows considerable variation, particularly in leaf and phyllary shape and size and pubescence. Four hundred seventy-six herbarium specimens were measured for eight characters (Martin, 1958) and the variation showed no clinal tendencies. The irregular pattern of variation was concluded to result primarily from ecological modification of the phenotype. A number of specimens with extremely broad

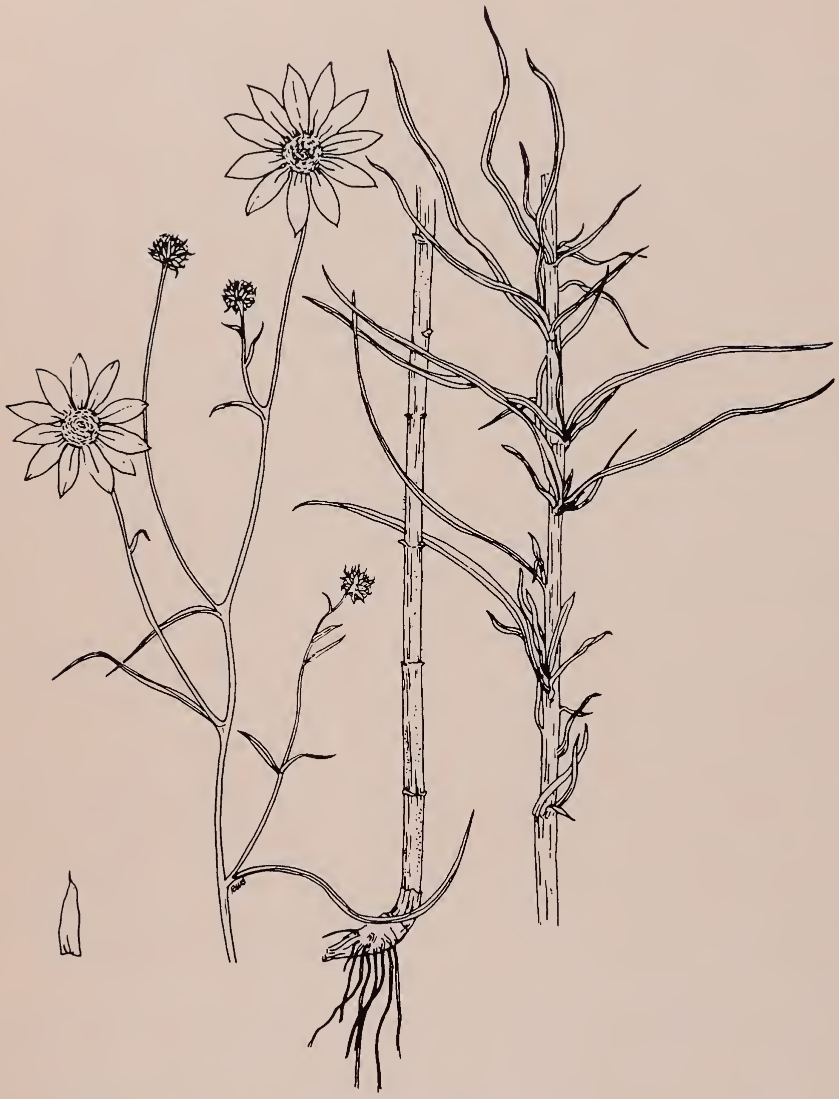


Fig. 43. *Helianthus angustifolius*

leaves were recorded as growing in dense shade. Watson (1929) had concluded that habitat could have a profound effect upon phenotype in this species. Hybridization could also account for some of the variation but considering its wide range there is on the whole very little evidence for hybridization with other species excepting *H. floridanus.*

Helianthus angustifolius is closely related to *H. floridanus.* Although the extreme form of that species is a very distinct plant, in general possessing shorter and much broader leaves which are usually conspicuously undulate and lacking crown buds, the two are connected by a series of intermediate specimens in northern Florida and southern Georgia which have been somewhat arbitrarily assigned to one or the other species. The artificial hybrid between the two is as fertile, or nearly so, as the parental species.

Helianthus angustifolius is also closely related to *H. simulans*, if indeed the two are different species. The extreme forms are quite distinct when growing side by side in the greenhouse, but separation of herbarium material is another matter. The differences between the two are discussed under *H. simulans.* The artificial hybrid between these two "species" also shows very high pollen fertility although there is some reduction in seed set. Certainly a strong case cannot be made for considering *H. floridanus* and *H. simulans* as distinct species. However, certain important evolutionary considerations would be obscured if they are not given recognition. Perhaps the non-committal category of variety should be employed here as a sign of ignorance of the real relationship.

The presence of crown buds, the leaf dimorphism, the stem pubescence and the disk and style-branch color of *H. angustifolius* suggest a relationship to *H. heterophyllus.* The narrow leaves of *H. salicifolius* superficially resemble those of *H. angustifolius* but are flat and entire or serrulate and glabrous or nearly so. In addition the phyllaries differ as do the underground systems. The artificial hybrid between the two species is difficult to secure and shows some reduction in fertility. Thus the two species do not appear to be particularly closely related.

A photograph from the British Museum of the same plant figured by Fernald as the type (Rhodora 49. pl. 1084. 1947.) bears the annotation "Syn Type Specimen/*Rudbeckia angustifolia* L." and is apparently the type of *Coreopsis angustifolia.* There is not much question that this plant is *H. angustifolius.* The photograph from British Museum bearing the annotation as the type of *Helianthus angustifolius* shows a plant with much broader leaves and is also probably referable to *H. angustifolius* as interpreted here. At least, from the photograph it is impossible to associate it with any other species. There are no specimens of *H. angustifolius* in the microfiche edition of Linnaeus herbarium (International Documentation Centre) and the one specimen of *Rudbeckia angustifolia* (1025.9) resembles *Helianthus schweinitzii.*

Rudbeckia angustifolia and *H. angustifolius* are continued as separate species through the third edition of Species Plantarum. I have not made a detailed search as to who first combined the two species, although Gray treated them as one (1884).

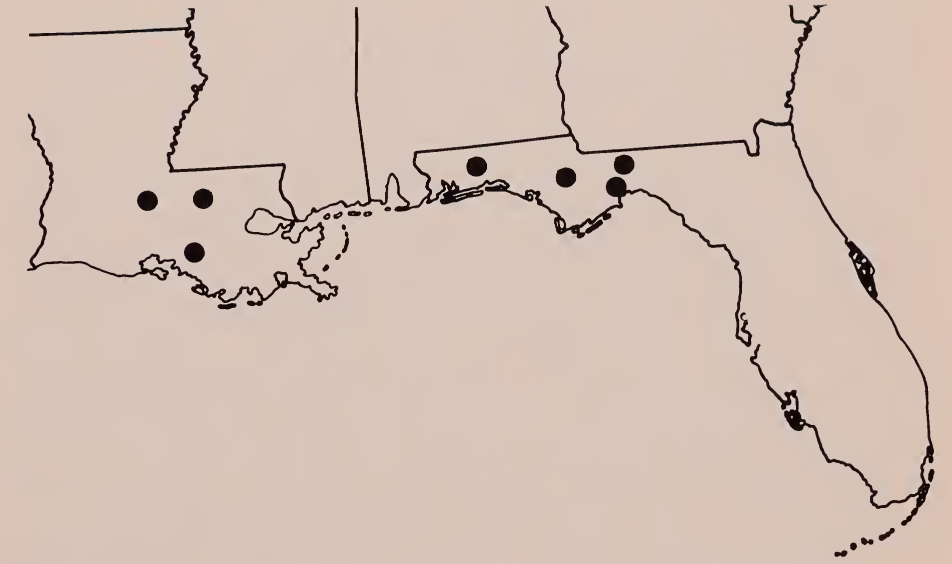
The two varieties are both based on broad leafed individuals. The variety *nemorosus* probably is a plant showing influence of *H. floridanus* while variety *planifolius* may well be a shade-induced form. That genetic differences in leaf shape exist is clear, however, from the cultivation of plants in the greenhouse. Plants showing the same leaf type as var. *planifolius* from Arkansas are recorded as growing in open situtations.

Although this is a wide ranging species, hybrids, as mentioned above, appear to be rather rare. The very late blooming of *H. angustifolius* probably serves as an effective barrier to hybridization with most of the other sympatric species. Hybridization certainly occurs with *H. floridanus* and hybrid swarms have been found by Martin in Georgia. Some specimens have been seen that suggest hybrids with *H. heterophyllus* and *H. salicifolius*. On the other hand, the natural hybrid with *H. atrorubens* previously listed by us (Martin, Smith and Heiser, 1962) has been reidentified as *H. schweinitzii* and the natural hybrids with *H. maximiliani*, which were based on cultivated plants, now seems unlikely (see under *H. simulans*).

Artificial hybrids have been secured with *H. atrorubens*, *H. floridanus*, *H. longifolius*, *H. maximiliani*, *H. radula*, *H. salicifolius* and *H. simulans*. With the exception of the hybrids with *H. floridanus* and *H. simulans* fertility is moderately to highly reduced, although chromosome pairing is generally regular or nearly so. A sterile hybrid was also secured with *H. niveus* ssp. *canescens*.

44. Helianthus simulans E. E. Wats., Pap. Mich. Acad. Sci. 9:363. 1929. (T.: Louisiana, *Watson* 715, MSU!)

Roots numerous, larger somewhat thickened upward, others cord-like; rhizomes thick (to 1 cm.) 5-10 cm. long; stem (0.6-) 1.5-2.6 m. tall, stout, strigose-hispid to strigose or somewhat short-hirsute; axillary fascicles usually present; basal leaves obovate, tapering to short petiole; cauline leaves alternate, or nearly all opposite in small individuals, subsessile, linear-lanceolate to broadly lanceolate, slightly revolute or flat, entire or remotely serrulate, dark green and scabrous above, lighter green and hispidulous to tomentulose below, mid-vein prominent, 9.0-22.0 cm. long, 0.7-4.0 cm. wide; heads usually numerous in corymbose or sometimes racemose arrangement; disks 1.3-2.0 cm. in diam.; phyllaries lanceolate, loose, acute to short attenuate, sparingly short-hairy 1.5-2.0 mm. wide, about equalling disks; rays 15-23, 1.6-3.0 cm. in length; lobes of disk corollas purple or yellow, style branches



Map 44. *Helianthus simulans*

yellow, anthers black; pales subentire to 3 to 5 short cuspidate; achenes glabrous, 2.5-3.0 mm. long.

Chromosome number: n = 17

Distribution: Florida and Louisiana. Oct.-Nov.

As comparisons of the descriptions will show, this species differs very little from *H. angustifolius* and *H. floridanus*. The leaves have been used for the key characters to separate them since the whole plant is seldom present on herbarium sheets. However, the most striking difference between *H. simulans* and these other species is that it is a much more robust plant, frequently twice as tall and with stems and rhizomes twice as thick.

This plant first became known to me in 1957 when Martin and Smith collected a plant growing in a yard in Mt. Dora, Lake Co., Fla., which appeared to combine features of *H. angustifolius* and *H. maximiliani*. Plants grown from seed of this plant, which would represent an F_2 generation or a backcross to an unknown plant, if the plant were a hybrid, were grown and showed considerable variation in leaf width and gave pollen counts of 0-60%. None of these plants closely resembled our artificial hybrids of *H. angustifolius* x *maximiliani*, but since they were not F_1's the possibility that they are of such hybrid origin is not ruled out.

Three years later a specimen and seeds of a plant from "banks of marsh at St. Mark's" Wakulla Co., Florida were received from Robert Godfrey who indicated that the plant was "probably naturalized from cultivation" and

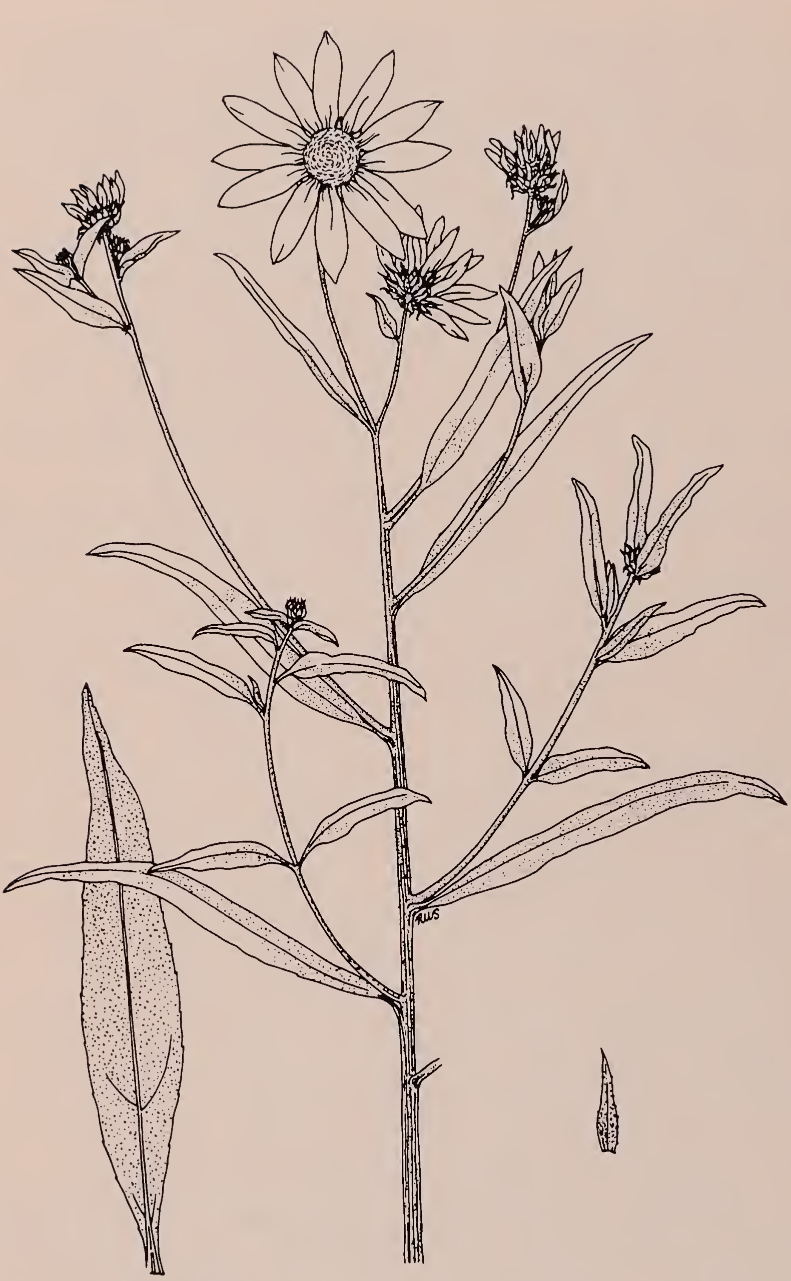


Fig. 44. *Helianthus simulans*

he reported that a similar sunflower was cultivated in yards in that area. Plants grown from these seeds again showed great variation in leaf size, both yellow and purple disks, and considerable variation in pollen stainability (from 40%-99%). However, all the plants were extremely tall and there were no segregates that approached any other species.

Crosses of these plants with high pollen stainability were made with each other and with *H. agrestis*, *H. atrorubens*, and *H. angustifolius*. The sib crosses gave plants very similar to the parents, and with pollen stainability again showing a great range (33%-99%). The hybrids with *H. agrestis* produced perennials which failed to develop normal flowers and produced no pollen (Heiser, 1965 as *H. floridanus*); those with *H. atrorubens* showed pollen stainabilities ranging from 75 to 85% and gave very few seeds in sister crosses; whereas those with *H. angustifolius* gave pollen stainabilities of over 90% and about 50% seed set.

Certain additional collections made by Godfrey and shown on the map, although differing considerably from the St. Mark's plant, also appear to belong to this same "species."

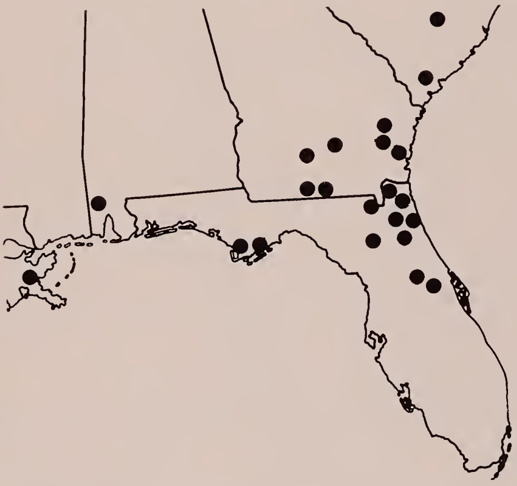
At this time a rechecking of Watson (1929) revealed that his *H. simulans*, which we had previously considered a yellow disked variant of *H. angustifolius* was very similar to the Florida material except for the somewhat narrower leaf. Watson reported that the species "invariably grows in wet, black muck." He gives the type as *Watson 715*, between Cade and St. Martinsville (St. Martin's Parish) but plate XLIX labeled "type" gives Washington (St. Landry Parish). Watson cites other plants from Louisiana which have not been seen, and *McCoy 2* and *3* from the campus of Southern University (East Baton Rouge Parish) in the New York Botanical Garden, according to notes made some years ago, are very similar to the Florida material, although the date given, "June 27" is completely out of line with the other collections; in fact, it is too early for any perennial species.

Thus we are presented with one of the little botanical mysteries that makes taxonomy both interesting and frustrating. A detective at this stage might come up with several theories but obviously he would need more facts before he would be able to arrive at a satisfactory answer. However, what appear to be the most likely theories may be presented. Both assume that the Louisiana material and the Florida material are indeed the same, which, of course, is hardly proven. First, we might consider that *H. simulans* is a native species of Louisiana and possibly Florida and that, appreciated for its showiness, was introduced into cultivation. For explanations of the variability in the Florida collections and the low fertility of some plants we might postulate hybridization with *H. angustifolius*, although that does not satisfactorily account for the broad leaves of some individuals. Or, we might assume that this species owes its origin to hybridization of *H. angusti-*

folius with some other species and that hybrid derivatives have become more or less stabilized, some of which are cultivated and some of which have escaped. The other parent could well be *H. maximiliani* since the ways in which this species differs from *H. angustifolius* are in the direction of *H. maximiliani*—general aspect, size, occasional racemiform arrangement of heads. *Helianthus maximiliani*, although not naturally overlapping the range of *H. angustifolius*, is a species frequently cultivated as an ornamental. The lack of herbarium records from the south does not mean that it isn't cultivated there, since few plants from yards enter herbaria. The fact that all collections of *H. simulans* date from 1926 argues for a fairly recent origin except that it must be realized that this sunflower comes from an area not too well known botanically until recently. It must also be admitted that it is entirely possible that certain specimens which we have previously annotated as *H. angustifolius* may, in fact, be *H. simulans*.

45. Helianthus floridanus A. Gray, ex Chapman. Fl. S. U.S. 2nd ed. p. 629, 1883. (T.: Florida, *Palmer 283*, GH!)

H. undulatus Chapman, Fl. S. U.S., 3rd ed., p. 253, 1897. (T.: W. Fla. *Chapman*, GH)



Map 45. *Helianthus floridanus*

Roots fibrous, rhizomes long and slender to medium-slender; crown buds rarely present; stem erect, 1-2 m. in height, usually much branched, scabrous-hispid to hispidulous, pubescence often more dense at base; lower-most leaves opposite, essentially similar to cauline leaves, cauline leaves usually alternate, blades lanceolate, oblong or sometimes ovate, usually obtuse, 1-3 nerved, short petiolate or sessile, scabrous above, somewhat scabrous to tomentulose

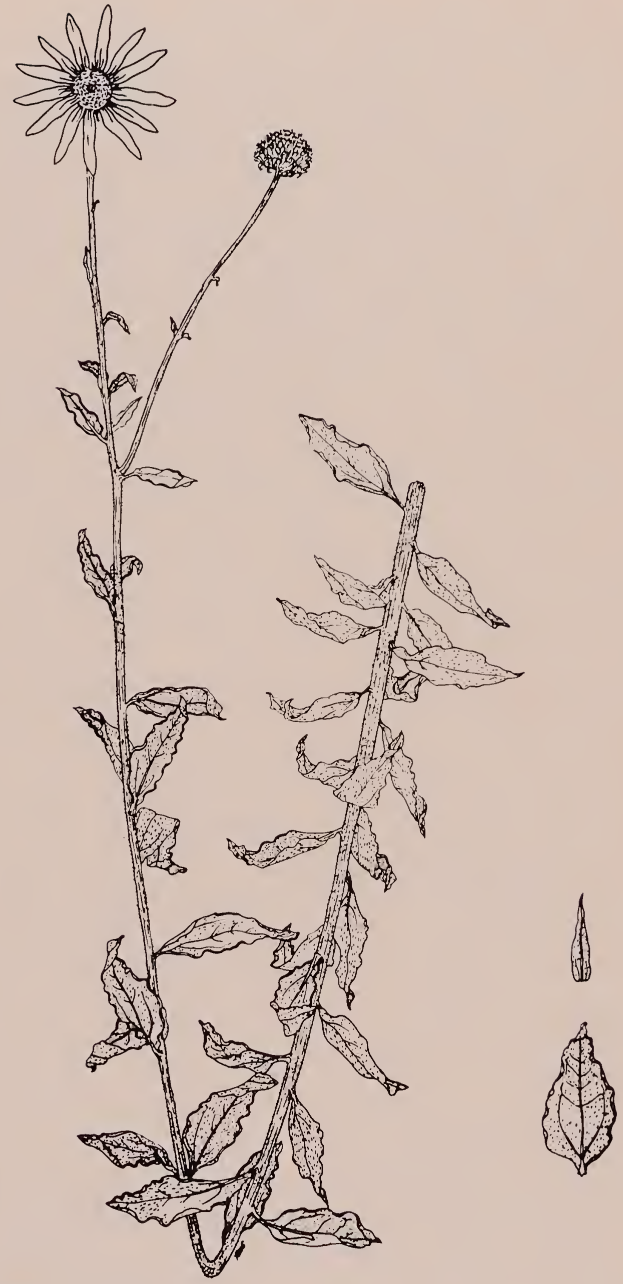


Fig. 45. *Helianthus floridanus*

below, revolute, undulate or flat, usually entire, rarely serrate, 4.0-15 cm. long, 0.5-6.0 cm. wide, seldom more than 5 times as long as broad; heads one to few in a loose panicle; disk 1.2-1.4 cm. in diameter; phyllaries lanceolate, acute to acuminate or outer rows occasionally nearly obtuse, usually not exceeding the disk, often loose, rarely slightly reflexed, hispidulose to hispid, 5.0-9.0 mm. long, 1.5-2.5 mm. wide; lobes of the disk corollas purple or yellow, glabrous, base of throat slightly pubescent; pales entire or nearly so, the tip usually purplish, subglabrous, slightly keeled; achenes ca. 3 mm. long.

Chromosome number: n = 17

Distribution: In sandy soils, South Carolina to north Florida, west to southern Alabama.

The extreme form of *H. floridanus* with rather broad, undulate, sessile or subsessile, scabrous leaves is quite distinct from other species but as can be seen from the description there is great variation in the leaves, and some plants are found which are transitional to *H. angustifolius.* Martin found hybrid swarms in Georgia and this, coupled with the fact that artificial hybrids are fertile, indicates that hybridization is probably the cause of the intergradation. Although one cannot arrive at a satisfactory solution of the past history of this species from a study of the plants as they exist today, one may assume that the two species differentiated in isolation and came into contact subsequently. It appears that the more aggressive *H. angustifolius* is in the process of replacing *H. floridanus* through hybridization (Heiser, 1961b) so that the "pure" form of *H. floridanus* is becoming rare. It could, of course, be assumed that the two have never reached the species level and that they should not be accorded specific rank. However, as the map reveals they can hardly be considered geographical races. Whether or not there are any marked ecological differences between the two is not definitely known, but apparently there are not. As Fernald (1947) remarked, "its root system and phyllaries seem to indicate a true species—as species go in *Helianthus.*"

In addition to the artificial hybrids mentioned above, hybrids with reduced fertility have been obtained with *H. longifolius* and essentially sterile hybrids with *H. debilis.*

Series 5. Atrorubentes

Roots fibrous or cord-like; rhizomes usually lacking; basal rosette usually present; stem leaves often few and reduced in size; phyllaries mostly 3-5 mm. broad; lobes of disk corolla purple, except in *H. carnosus*; achenes 3-5 mm. long, often black; mostly species of southeastern United States.

Key to Species of Atrorubentes

Lobes of disk corolla yellow; stem and leaves glabrous; leaves linear or nearly so . 50. *H. carnosus*

Lobes of disk corolla red or purple; stems and leaves pubescent; leaves broader (except cauline leaves of *H. heterophyllus* sometimes linear)

Cauline leaves usually highly reduced, often bract-like or if well developed, linear or narrowly lanceolate

Rays lacking or only 1-2 mm. long; basal leaves obovate to orbicular; cauline leaves mostly bract-like .... 49. *H. radula*

Rays 14 mm. or more long; basal leaves ovate or elongate-oblanceolate or spathulate; cauline leaves linear or narrowly lanceolate .... 48. *H. heterophyllus*

At least lower cauline leaves well developed, rather similar to basal leaves

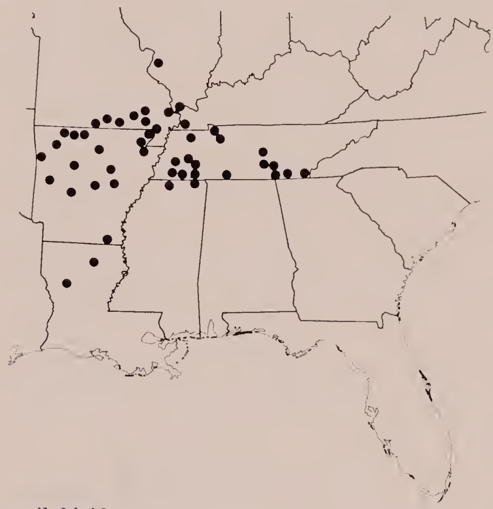
Leaves becoming quite reduced in size in upper 1/2 or 2/3's of stem; petioles often nearly as long as leaf, often winged, frequently hirsute .... 47. *H. atrorubens*

Leaves becoming gradually smaller upward; petioles much shorter than leaf, not winged, scabrous to glabrous .... 46. *H. silphioides*

46. Helianthus silphioides Nutt. Trans. Amer. Phil. Soc. N.S., 7:366. 1841. (T.: Plain of the Arkansas, *Nuttall*, BM, Photo GH!)

H. atrorubens var. *pubescens* Kuntze, Rev. Gen. 2:343. 1891. (T.: Alexander Co., Ill. *O. Kuntze 2870* NY!)

H. kentuckiensis McFarland & Anderson, Amer. Midl. Nat. 9:139. 1924. (T.: Clinton Co., Kentucky. *McFarland & Anderson 374*, MO!)



Map 46. *Helianthus silphioides*

Rhizomes absent or poorly developed, large crown buds present; stems several, 1.5-3.0 m. tall, branched above, hispid to hispid-strigose below, glabrate above; leaves ovate to suborbicular, truncate to subcordate, and abruptly contracted to the short petiole, thick, and firm, serrate to crenate, very scabrous both surfaces, seldom somewhat strigose, 10-15 cm. long,

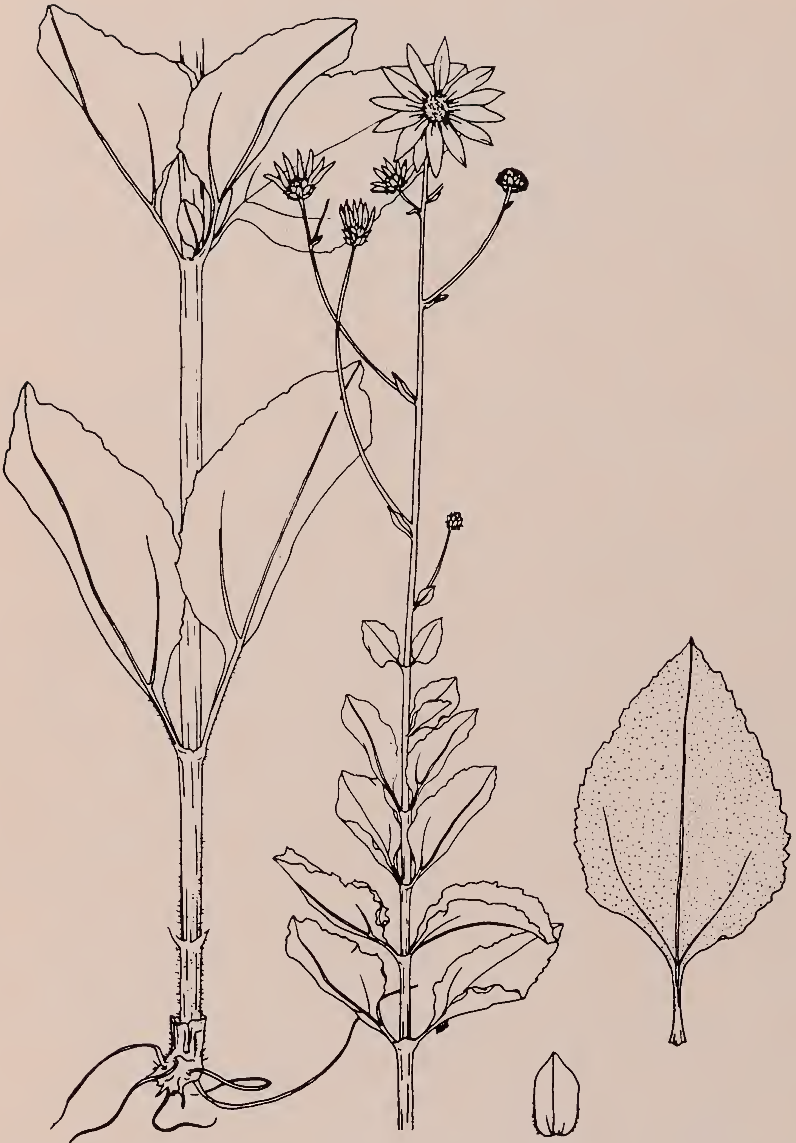


Fig. 46. *Helianthus silphioides*

7.5-15 cm. wide, lower opposite, upper becoming gradually reduced in size and opposite or sometimes alternate; petioles less than one half as long as blade, usually very short and relatively slender or upper leaves sessile; heads numerous on long to short bracteate peduncles; disk 1.0-2.0 cm. in diam.; phyllaries oblong to oblong-ovate, obtuse to acutish, generally glabrous or nearly so, sometimes ciliolate on margins, often purple veined, appressed, graduated, outermost much shorter than disk, 3-5 mm. wide; rays usually 12-14, to 2 cm. long; lobes of disk-corollas dark red to red; style branches yellow or purple; chaff shallowly 3-cuspidate to entire, keeled, puberulent toward apex; achenes 3-4 mm. long, pubescent only at summit.

Chromosome number: n = 17

Distribution: In open or semi-open places, Tenn. to southern Illinois and Missouri, south to Louisiana. Aug.-Sept.

Fernald (1946) deserves the credit for untangling the synonymy of this species. He, however, was incorrect in stating that this species was propagated by means of long rhizomes and was found in Indiana. His conclusions were based on *Kriebel 3965* which is *H. rigidus* ssp. *subrhomboideus.*

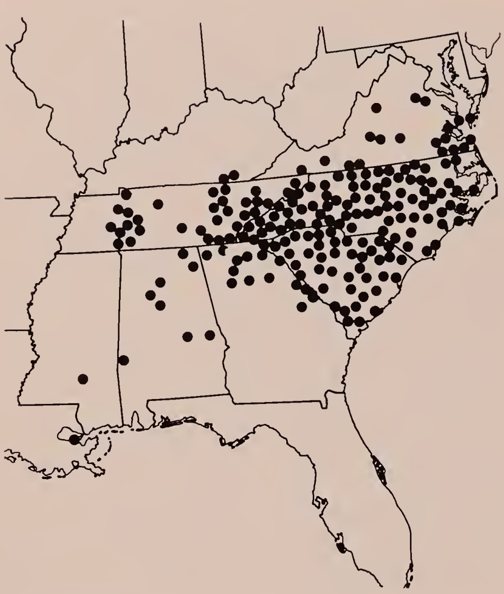
Except in the area of overlap with *H. atrorubens* in Tennessee (see discussion under that species) this is an extremely constant species, perhaps in part steming from its lack of hybridization with other species. Other than presumed natural hybrids with *H. atrorubens* and *H. mollis* in Tennessee no other hybrids are thus far known. Artificial crosses with several other species, excepting *H. atrorubens,* have been unsuccessful.

Since the original type of *H. kentuckiensis* in the McFarland Herbarium is no longer extant, the isotype at the Missouri Botanical Garden is designated the lectotype.

47. **Helianthus atrorubens L.** Sp. Pl. 2:906. 1753. (T.: Dillenius, Hort. Elth. p. 112, t. 94, f. 110. 1732. see Rhodora 48:75. 1947.)

H. sparsifolius Ell. Sketch 2:415. 1824. ("western district of Georgia")
H. atrorubens var. *normalis* Kuntze, Rev. Gen., 1:343. 1891.
H. atrorubens var. *atrorubens* Cronq. Rhodora 47:399. 1945.
H. atrorubens var. *alsodes* Fern. Rhodora 48:74. 1946. (T.: Princess Anne Co., Virg., *Fernald, Long* and *Fogg* 5127, GH!)

Rhizomes absent or poorly developed; vegetative reproduction from bud at base of old plant, stems solitary or few, erect, 0.5-2.0 m. tall, often much branched, hispid-strigose, lower part often villous, glabrate above; basal leaves crowded, thick, opposite, usually obtuse, broadly lanceolate to ovate, serrate to crenate, generally cuneate and contracted at its base and broadly decurrent along the long petiole, long-strigose-hispid below, scabrous hispid



Map 47. *Helianthus atrorubens*

above, hairs of midrib long, blade 8.0-26.0 cm. long, 3-10 cm. wide, lower petioles often as long as blades; mid and upper cauline leaves much reduced, opposite but sometimes becoming alternate, widely separated; heads several on long bracteate peduncles; disk 0.8-1.5 cm. in diam., phyllaries ovate-lanceolate to oblong, obtuse to acute, rarely mucronate, glabrous, sometimes with ciliolate margin, often purple veined, graduated, outermost shorter than disk, 3-5 mm. wide, not reflexed; rays orange-yellow, 10-15 usually not exceeding 2.0 cm. in length; lobes of disk florets dark red; style branches yellow or purple; pales linear, entire, or nearly so, narrowly acuminate, puberulent or glabrous; achene pubescent only at the apex, ca. 3 mm. long.

Chromosome number: $n = 17$ (fragments sometimes present)

Distribution: Commonly in open woods and dry, partially shaded hillsides from Virginia south through Georgia and west to Kentucky and Louisiana. Aug.-Oct.

Helianthus atrorubens is most closely related to *H. silphioides* which replaces it to the west. It is distinguished from that species by a more densely pubescent stem, fewer and smaller stem leaves, basal leaves usually less ovate and the usually solitary stems. In central Tennessee, a number of specimens collected by Janice Beatley (1963) are somewhat intermediate and difficult to place in one species or the other. While it might be possible that this is the result of primary intergradation in the sense of Mayr (1942), it is equally or more probable that it is secondary intergradation or hybrid-

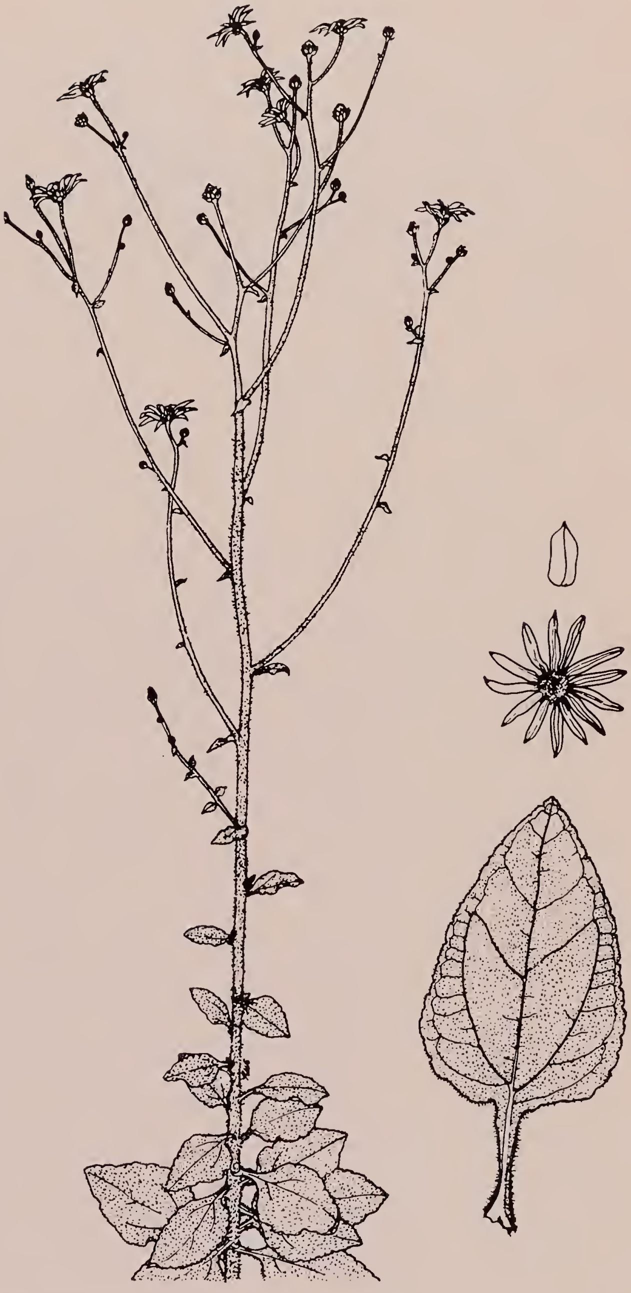


Fig. 47. *Helianthus atrorubens*

ization between two species which have differentiated in isolation and recently come into contact. *Helianthus atrorubens* is primarily a species of the Appalachian region whereas *H. silphioides* is concentrated in the Ozark area.

Since *H. atrorubens* and *H. silphioides* are rather similar, for the most part allopatric, and intergrade where they have overlapping distribution, these taxa might well be considered subspecies of one species. However, as Fernald (1946b) remarked, these two species seem as distinct as any two in the genus. Moreover, the artificial F_1 hybrids show some reduction in fertility so we have chosen to maintain them as species.

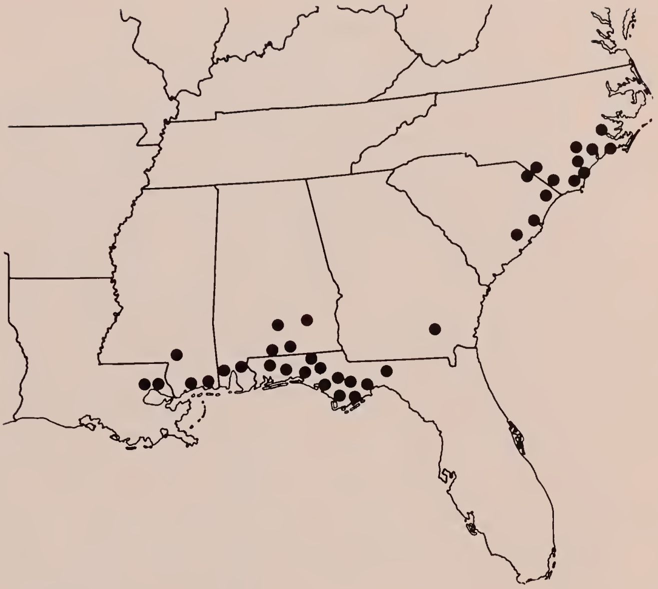
This species shows considerable variation in leaf shape, and plants from the northern part of the range tend to be more leafy and to produce leaves with shorter and more broadly winged petioles. From experimental garden cultures it has been found that the leaves on the same plant vary from year to year so it is probable that much of the leaf variation is environmental modification, although some of the difference between strains must be genetic. Fernald's var. *alsodes* is one of the extreme forms, but since it may occasionally occur with the typical form throughout much of the range, it hardly deserves recognition. Elliott's *H. sparsifolius,* like several of his species of this genus, is somewhat difficult to place. The description fits *H. silphioides* nearly as well as it does *H. atrorubens,* and it is in synonymy here chiefly because the geographical source falls within the range of the latter species.

In addition to the probable hybrids with *H. silphioides,* natural hybrids are also known with *H. longifolius,* and a few herbarium specimens have been seen which appear to represent hybrids with *H. divaricatus, H. microcephalus, H. mollis* and *H. occidentalis.* Artificial hybrids have been secured with *H. giganteus, H. grosseserratus, H. heterophyllus, H. mollis, H. radula, H. salicifolius, H. silphioides* and *H. simulans.* Although all of these hybrids are vigorous and normal, except for those with *H. radula* which failed to flower and those with *H. salicifolius* which produced abnormal heads, the pollen stainability is usually less than 50%. Seventeen pairs of chromosomes, however, were regularly observed in most of the hybrids.

48. Helianthus heterophyllus Nutt. Jour. Acad. Sci. Phil. 7:74. 1834. (T.: *Gates,* PA!)

H. gracilis Bertoloni, Misc. Bot., 7:41. 1848.
H. elongatus Small, Fl. S.E.U.S. 1266. 1903. (T.: Fla. Wakulla Co., *Nash 2541* NY!)

Rhizome lacking or a very condensed nearly erect structure which gives rise to new plants or these coming from the roots; stems usually single, stiffly erect, 0.5-1.2 m. tall, rarely branched above, hispid to somewhat hirsute, rarely nearly glabrous; basal leaves closely crowded, rosette-like, ovate to



Map 48. *Helianthus heterophyllus*

more frequently elongate-oblanceolate or spathulate, acute to occasionally acuminate, entire or obscurely serrulate, often conspicuously three-nerved, hispid-hirsute, usually more densely so above, 6.0-27.6 cm. long, 1.2-4.3 cm. wide, decurrent on petiole; cauline leaves becoming narrowly lanceolate or linear, opposite or subopposite, bract-like near heads and frequently alternate, scabrous-hispid to hispid-hirsute, frequently revolute margined; heads 1-5, usually solitary; disk 1.5-2.5 cm. in diam.; phyllaries lanceolate to ovate-lanceolate, acute to somewhat acuminate, slightly hispid to subglabrous on backs, sometimes short ciliate on margins, erect or outermost somewhat reflexed, equalling or slightly exceeding disk, 2.0-3.5 (-5.0) mm. wide; rays 12-14, 14-36 mm. long; lobes of the disk-corolla purple, glabrous or pubescent; anthers and stigmas purple; pales shallowly 3-cuspidate to entire, keel usually ciliate, tip purple and glabrous; achenes slender, black, 4-5 mm. long; pappus of 2 awns, sometimes 3-cuspidate, squamellae occasionally present.

Chromosome number: n = 17

Distribution: low wet sandy usually acid soils, coastal plain from North Carolina to Louisiana, Aug.-Oct.

Since this species is intermediate in many features, excepting the phyllaries, between *H. angustifolius* and *H. radula* and is sympatric over much of its range with these species, at one time the thought of a hybrid origin was entertained. The artificial hybrid between these other two species, however,

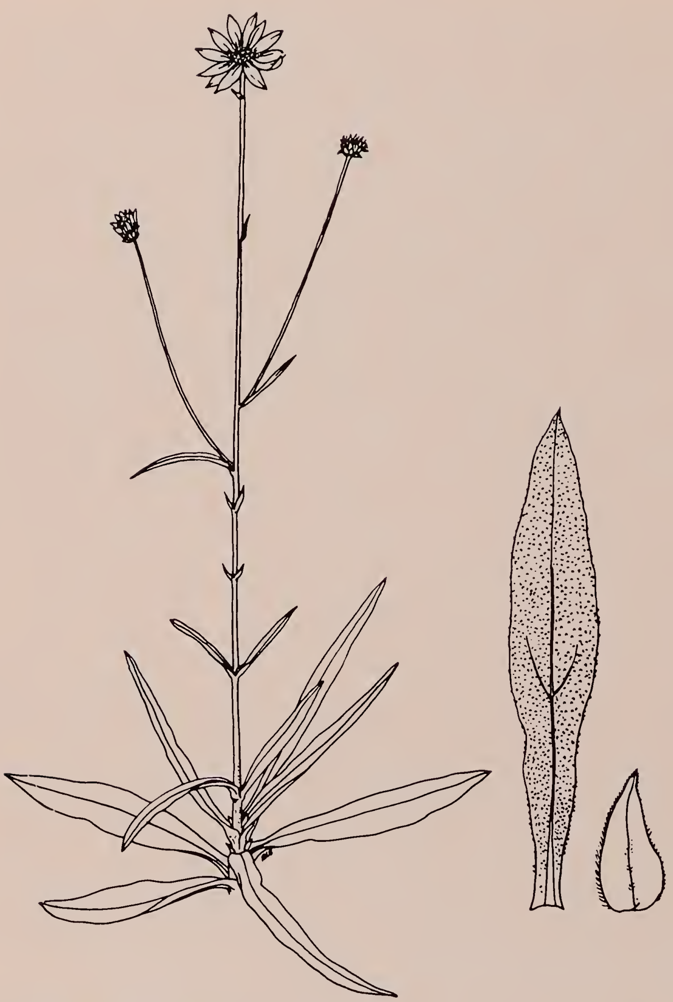


Fig. 48. *Helianthus heterophyllus*

is very unlike *H. heterophyllus.* (The hybrid between *H. carnosus* and *H. radula* is rather similar to this species except for the softer pubescence.) While, of course, it is possible that certain recombinants out of hybridization might produce plants similar to *H. heterophyllus,* it seems much more likely that this is a fairly old species whose distribution follows the ancient coast line. This, of course, assumes that the colonies in the one county in Georgia are relic ones and do not represent recent introductions.

The species today has a largely discontinuous distribution, but no logical basis has been found for the taxonomic separation of the eastern populations from the more southwestern ones. There is some variation in the size and shape of the leaves, particularly in the southwestern portion of the range, and some variation in pubescence, phyllary shape, and head size.

Many plants of the species have been examined which show pollen fertilities between 50% and 75% instead of the usual 90% or more found in the other diploid species, and many plants have been found which show highly reduced seed set. The cause of this is unknown. Although we had earlier reported meiotic abnormalities and suspected triploidy (Heiser and Smith, 1955), five additional collections have been examined, all of which have regularly shown 17 pairs of chromosomes.

In addition to the putative hybrids with *H. angustifolius,* one plant has been found (*Heiser 4661*) which may be a hybrid with *H. radula.* This individual was transplanted to the greenhouse and crossed with *H. radula.* The fertility of the putative hybrid was not determined but pollen stainabilities on the progeny ranged from 36% to 55%. Attempts at artificial hybridization between *H. radula* and *H. heterophyllus* gave fairly good seed set, but of six seedlings secured, five died at an early stage and the sixth before it had flowered. *Helianthus heterophyllus* has proven a difficult species for greenhouse culture and for this reason it has not been possible to attempt other hybridizations.

The relationships of this species are obscure and it probably comes out of the same stock that gave rise to *H. radula* and perhaps other southeastern perennials. It is a fairly distinct species with the leaf shape, the harsh pubescence, and the highly reduced opposite stem leaves setting it off fairly well from other species of the area.

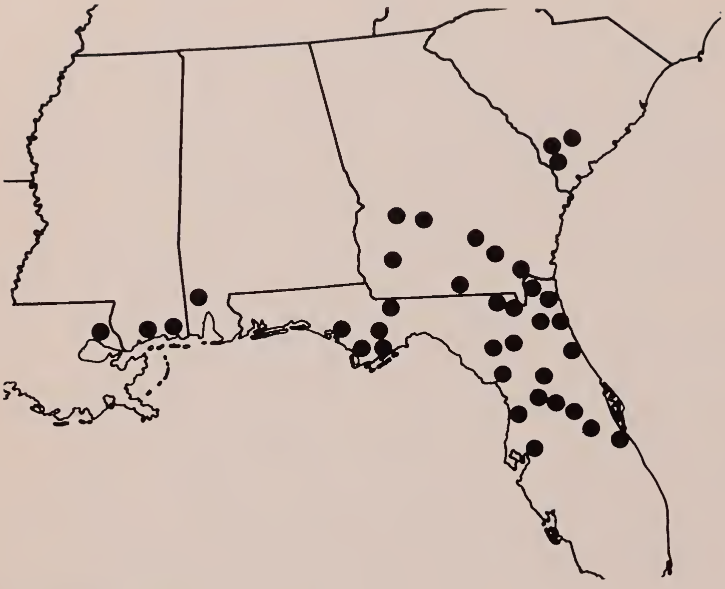
49. Helianthus radula (Pursh) Torr. & Gray, Fl. N. Am. 2:321. 1841.

Rudbeckia radula Pursh, Fl. 2:575. 1816. (T.: Georgia, *Bartram,* BM)

Rudbeckia apetala Torr. ex Nutt. Jour. Acad. Sci. Phil. 7:77. 1834. (T.: Alab., *Gates* PA!)

Neactelis strigosa Raf. Neobot. 69. 1836.

H. apetalus Leconte ex Nutt. Trans. Am. Phil. Soc., N.S., 7:356. 1841. (as synonym)



Map 49. *Helianthus radula*

Echinomeria apetala Nutt., *l.c.*
Rudbeckia nudiflora Bertoloni, Misc. Bot. 7:39. 1848.

Rhizomes lacking; stems one to several from rosette, becoming erect, 0.5-1.0 m. tall, usually unbranched, sparingly hirsute to glabrous above, usually densely hirsute below, leaves mostly in basal rosette, obovate to orbicular, obtuse, entire or serrulate with widely spaced teeth, scabrous-hispid to somewhat hirsute above, strigose-hispid to hirsute below, 4.6-11.3 cm. long, 2.1 to 9.6 cm. wide, blade decurrent to the base or very short petiolate, cauline leaves few or lacking, extremely reduced, spathulate and opposite below, becoming bract-like and alternate above; heads nearly always solitary; disk 1.5-2.5 cm. in diam.; phyllaries lanceolate to oblong or ovate-lanceolate, acute to acuminate, glabrous to hispid, dark purple, usually appressed, about equalling disk, 3-4 mm. wide; rays lacking or much reduced, 1-2 mm. long, purple to purplish-yellow; disk-flowers dark purple, stigmas purple; pales acute or acuminate, generally entire, glabrous or essentially so, green-below, purple above; achene black, somewhat concave at apex, 3-4 mm. long, essentially glabrous except at summit, pappus of two linear-lanceolate awns, ca. 3 mm. long.

Chromosome number: $n = 17$

Distribution: Low, sandy, generally open pine-barrens from North Carolina to central Florida to eastern Louisiana. Sept.-Nov.

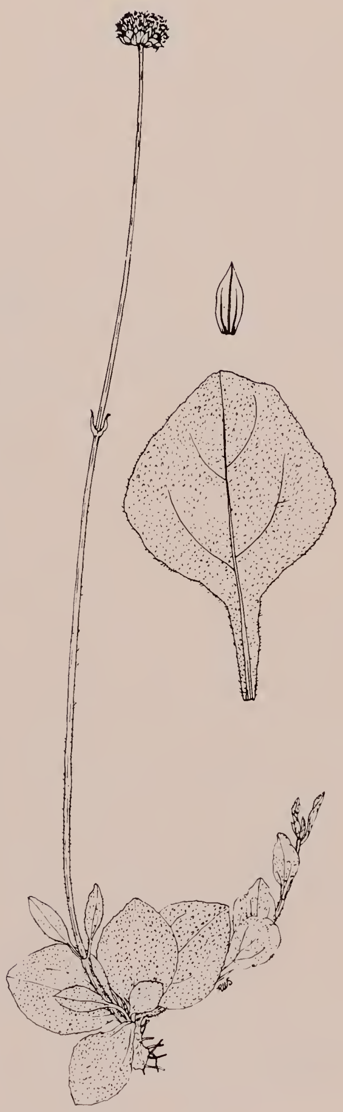


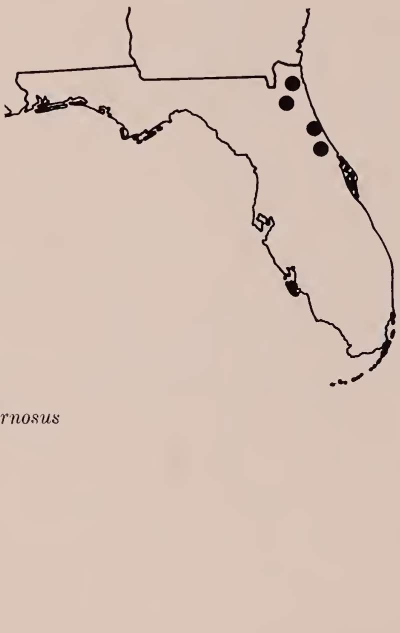
Fig. 49. *Helianthus radula*

This very distinctive species is easily recognized by the absence of, or the highly reduced, rays, the deep purple heads, and the broad pubescent leaves mostly confined to the base of the plant. Absence of rays is rare in *Helianthus*. Rayless forms of *H. annuus* have appeared in garden cultures presumably the result of mutation and Dr. D. M. Smith has seen rayless forms of *H. ciliaris* in Texas. It would be interesting to know if the pollinators of this species differ from those of the others. Although Watson (1929) considered this a rare species it actually occupies a considerable range and it is frequently abundant in many of the areas where it grows.

Its closest relatives are perhaps *H. atrorubens* and *H. heterophyllus* and to a lesser extent *H. carnosus*. Its distribution is largely sympatric with *H. heterophyllus*, although it occupies a considerably larger range in Florida than does that species, and it is almost completely allopatric with *H. atrorubens* which replaces it to the north. One might suggest that it differentiated at a time when Florida was separated from the mainland and has now spread into the same areas occupied by *H. heterophyllus* which may have been confined to the old coast line of the mainland at the time when the separation occurred.

Its late blooming has limited the number of species with which artificial hybridization has been attempted. By using artificial short days it was induced to flower and successful hybrids were obtained with *H. carnosus*. Vigorous hybrids were also obtained with *H. angustifolius* which, while showing considerable reduction in fertility, displayed regular meiosis. Hybrids obtained with both *H. atrorubens* and *H. heterophyllus* died before flowering. The only putative natural hybrid known is with *H. heterophyllus* from Georgia.

50. Helianthus carnosus Small, Torreya 2:75. 1902. (T.: Fla., Duval Co., *Lighthipe 320*, NY!)



Map 50. *Helianthus carnosus*

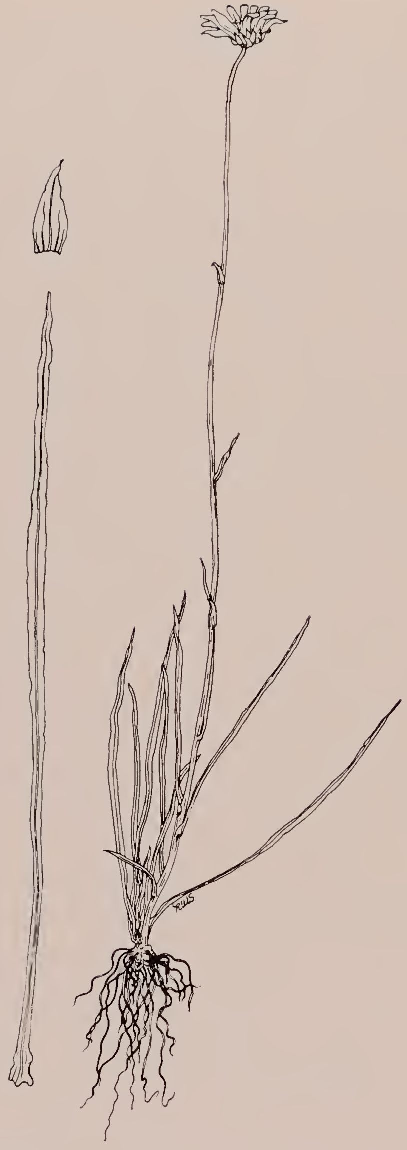


Fig. 50. *Helianthus carnosus*

Rhizomes lacking, crown buds present; stems to 0.6 m. tall, unbranched, glabrous, arising from an enlarged base which produces a cluster of leaves on one side and the erect stem on the other, usually red to purple; basal leaves in rosette, narrowly linear-oblanceolate to narrowly spathulate with a single prominent vein, glabrous, somewhat succulent, 4.0-20.0 cm. long, 0.5-1.5 cm. wide, blade narrowly decurrent to the base; leaves of the stem alternate, few, linear-lanceolate and highly reduced in size; heads usually borne singly; phyllaries oblong-lanceolate to ovate-lanceolate, acuminate, about as long as the disc, green with purple veins, mid-vein pronounced, slightly loose but not reflexed, glabrous or rarely puberulent 3.5-6.0 mm. wide; disk 1.7-2.4 cm. in diam.; rays 2.0-3.0 cm. long; lobes of the disk-corollas yellow, glabrous; the pales large, keeled, shallowly 3-cuspidate, glabrous; achenes black, glabrous, 3 mm. long.

Chromosome number: $n = 17$

Distribution: In rather wet, sandy soil, northeastern Florida; June to Sept.

This rather rare and very unusual species has leaves somewhat similar to *H. longifolius*; but the nearly naked "stems" and the characteristics of the head suggest a closer relationship to *H. radula* and *H. heterophyllus*, from which it is readily distinguished by the yellow disks and glabrous condition. Whether or not the word stem should be used in the description of this species is highly questionable, and it might be better to consider the species as having only a highly condensed stem at the base and refer to the erect portion as a peduncle or scape.

In parts of its range this species grows in close association with *H. radula* but natural hybrids between the two are unknown. The difference in time of blooming is perhaps an effective barrier, but where roadside mowing is practiced the plants of *H. carnosus* will bloom when the mowing is ceased which may permit an overlap in flowering periods with *H. radula*.

This species does not survive when grown in the field at Bloomington, but greenhouse culture has been quite successful. Artificial hybrids have been secured with *H. decapetalus* (2n), *H. longifolius*, *H. radula*, and *H. salicifolius*. The securing of hybrids would indicate that in spite of its very distinct morphology it is fairly closely related to the other eastern perennials. To account for its distinctiveness one might postulate that its ancestral stock was early isolated from the other perennials. Its present position, limited to Florida, might be used as evidence that it differentiated at a time when Florida was separated from the mainland. On the other hand, there is no real evidence as to its age and it might equally well be argued that it is a recently differentiated species which has become quite specialized.

Named Hybrids

H. x *ambiguus*: *H. giganteus* var. *ambiguus* T. & G. Fl. N. Am. 2:325. 1843. (T.: Long Island, Brooklyn, *Torrey* in 1841, NY!), *H. ambiguus* Britton, Man. 993. 1901, H. x *ambiguus* Long, Rhodora 56:202. 1954. (=*divaricatus* x *giganteus*)

H. x *brevifolius*: *H. brevifolius* Wats. Pap. Mich. Acad. 9:448. 1929. (T.: Ohio, Lake Co. *Hacker* in 1894, OS!), *H.* x *brevifolius* Jackson and Guard, Proc. Ind. Acad. Sci. 66:314. 1957. (=*grosseserratus* x *mollis*)

H. x *cinereus*: *H. cinereus* T. & G. Fl. N. Am. 2:324. 1843. (T.: Texas, *Drummond* NY!) (=*mollis* x *occidentalis* ssp. *plantagineus*), *H. cinereus* var. *Sullivantii* T. & G. Fl. N. Am. 2:324. 1843. (T.: Ohio, Columbus, *Sullivan* GH!) (=*mollis* x *occidentalis* ssp. *occidentalis*), *H.* x *cinereus*, Jackson and Guard, Amer. Midl. Nat. 58:428. 1957.

H. x *divariserratus* Long, Rhodora 56:200. 1954. (T.: Conn. Fairfield Co., *E. Watson* MSC!) (=*divaricatus* x *grosseserratus*).

H. x *doronicoides*: *H. doronicoides* Lam. Encyc. 3:84. 1789. (T.: Cult. P, photo IND!), *H.* x *doronicoides* Jackson, Rhodora 58:99. 1957. (=*giganteus* x *mollis*)

H. x *filiformis* (see *H. salicifolius*, p. 160)

H. x *glaucus*: *H. glaucus* Small, Bull. Torrey Club 25:480. 1898. (T.: North Carolina, Rowan Co., *Small* Aug. 12-27, 1894, NY!), *H.* x *glaucus* Smith & Guard, Brittonia 10:142. 1958. (=*divaricatus* x *microcephalus*)

H. x *intermedius* Long, Rhodora 56:201. 1954. (T.: Wisc., Brown Co., *Schuette* 9a5670, F!) (=*grosseserratus* x *maximiliani*)

H. x *kellermani*: *H. kellermani* Britt. Man. 994. 1901. (T.: Ohio, Franklin Co., *Kellerman* GH!), *H.* x *kellermani* Long, Rhodora 56:200. 1954. (=*grosseserratus* x *salicifolius*)

H. x *laetiflorus* (see p. 137)

H. x *luxurians*: *H. luxurians* E. E. Wats. Pap. Mich. Acad. 9:464. 1929. (T.: Ohio, Erie Co., *Watson 387* MSC!), *H.* x *luxurians* Long, Rhodora 56:201. 1954. (=*giganteus* x *grosseserratus*)

H. x *multiflorus* (see p. 118)

H. orgyaloides Ckll., Bot. Gaz. 67:264. 1919. (=*maximiliani* x *salicifolius*)

H. pilosus Tausch, Fl. 11:502. 1828. (probably=*giganteus* x *mollis*)

Names Not Satisfactorily Placed

H. divaricatus var. *scaberrimus* Wood, Classbook (ed. 1861). 449. 1861. =*H. hirsutus*?

H. hirsutus var. *pubescens* Wood, *l.c.* (based on *H. pubescens* Hook. Bot. Mag. 54:t.2778. 1827 which is probably *H.* x *doronicoides*) from the description given Wood's variety appears to be well within the range of *H. hirsutus* as interpreted here.

H. praetermissus E. E. Wats. Pap. Mich. Acad. Sci. 9:335. 1929. (T.: New Mexico: *Sitgreaves*, GH!). Known only from the type specimen which is somewhat fragmentary. Recent efforts to locate this sunflower in New Mexico have been unsuccessful (Heiser, 1958).

H. spathulatus Ell. Sketch. 2:421. 1824. see discussion under *H. resinosus*.

H. verticillatus E. E. Wats. Pap. Mich. Acad. Sci. 9:362. 1929. (T.: Tenn., Chester Co., *Bain* NY!) Known only from the type specimen. This specimen may well represent a hybrid derivative as suggested by Beatley (1963). She considers that *H. angustifolius* and *H. eggertii* may be involved in the parentage. It is more likely that it is a hybrid segregate of *H. grosseserratus* x *angustifolius*.

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